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CASPARY'S FUNGI FROM BALTIC AMBER: HISTORIC SPECIMENS AND NEW EVIDENCE

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Abstract

Amber is a valuable source of Mesozoic and Cenozoic fossil fungi. The earliest amber-preserved fungi were described in the 19th and early 20th century from Eocene Baltic amber. In 1907, Richard Klebs summarized the legacy of Robert Caspary based on his specimens, research notes, and publications. This treatise contains descriptions and illustrations of 13 morphologies of fossil fungi which have not been investigated since. We managed to locate six of Caspary's amber specimens and imaged and re-investigated the fossil fungi within. We provide amended descriptions of these six specimens, select new specimens from historic and recent collections which are likely conspecific with five fossils that appear to have been lost, and finally also describe and evaluate five newly found fossil fungi from Baltic amber. The fungi belong to the phylum Ascomycota (Subkingdom Dikarya). Only two of Caspary's fungi can be confidently assigned to modern genera, *Metacapnodium* (Metacapnodiaceae) and *Calicium* (Caliciaceae). The new combination *Calicium succini* (Caspary) Rikkinen and A. R. Schmidt is made. The fossils originally placed in *Acremonium*, *Cetraria*, *Gonatobotrys*, *Ramularia*, *Stilbum*, and *Torula* and cannot be assigned to these genera, and should not be used as minimum age constrains for the respective lineages.

FOSSILS in Baltic amber have been studied since the 19th century, but usually with a focus on arthropod and plant inclusions. The fungi have received far less attention, but given the life-like preservation, amber has recently proven to be a valuable source of fossil fungi and lichens (e.g. Schmidt *et al*. 2014; Kettunen *et al*. 2015, 2016; Kaasalainen *et al*. 2017).

The earliest descriptions of fungi from amber date back to the middle of the 19th century. Already in 1845 Heinrich Göppert and Georg Karl Berendt described *Sporotrichites heterospermus* and *Pezizites candidus* (Göppert & Berendt 1845) from Baltic amber. Soon after, Miles Joseph Berkeley (1848) described three species of filamentous fungi, and in 1858 Anton Menge described *Sphaerophorus moniliformis* also from Baltic amber. In 1886 Robert Caspary described several fungi and lichens from Baltic amber. He died in 1887, but the amber specimens were studied further by Richard Klebs, who in 1907 summarized Caspary's work on amber inclusions based on all available specimens, publications and unpublished manuscripts. This treatise (Caspary and Klebs 1907*a, b*) contains descriptions and illustrations of 13 morphologies of fossil fungi and represented the largest assemblage of fossil fungi known at that time. Some of the fungal specimens had already been described by Caspary (1886), but Klebs (in Caspary and Klebs 1907*b*) was the first to illustrate the fossils with line drawings (Fig. 1).

The fossil fungi included in Caspary and Klebs (1907*b*) have not been reinvestigated since, and as the original specimens were subsequently dispersed into different collections it has even become unclear which specimens are still available for study. Thus the true taxonomical affinities of the specimens are also open to question. When screening historic amber collections of the Museum für Naturkunde (Museum of Natural History) in Berlin and the Geoscientific Collections of the University of Göttingen, we managed to locate six specimens of Caspary's fungi. The remaining specimens seem to have been lost, but we were able to find new material of fossil fungi from other collections with morphologies that very closely correspond with those described by Caspary and later illustrated in Caspary and Klebs (1907*a, b*). These additional specimens confirm the presence of the diverse morphologies described 110 years ago from Baltic amber and provide better insights into micromorphology, reproduction and ecology than the relatively brief original descriptions and the sometimes vague line drawings of the lost specimens.

Here, we provide amended descriptions and photographic plates of Caspary's fungi, reanalyse their taxonomic affinities and briefly discuss their presumed palaeoecology. We also describe a number of new fungi, some of which closely resemble those illustrated in Caspary and Klebs (1907*a, b*), and others representing morphologies that have not been previously known

from Baltic amber. The combination of specimens from both historical and new collections enlighten the fungal diversity and composition of microscopic mycobiota of the Paleogene European amber forest.

MATERIAL AND METHODS

Origin and age of the amber specimens investigated

The fossils from historic (Table 1) and new (Table 2) collections are preserved inside 21 specimens of Baltic amber.

Baltic amber from the Baltic Sea region represents the largest amber deposit worldwide and has been known for many centuries. Today, most Baltic amber is mined in the Samland area near Kaliningrad, Russia, where it predominantly occurs in "Blue Earth" layers. These amber-bearing strata are Priabonian (c. 35 to 43 Ma) in age, but small amounts of amber also occur in Lutetian and Oligocene sediments, leading to a possible age range of *c*. 25 to 43 million years for all strata bearing Baltic amber (Kosmowska-Ceranowicz *et al*. 1997; Standke 1998; Kasiński and Kramarska 2008; Standke 2008). It is unclear whether the Oligocene amber represents redeposited Eocene material (Standke 2008); thus, a Lutetian to Priabonian age of Baltic amber is currently considered. Baltic amber eroded from these sediments is often found washed ashore along the coast of the Baltic Sea (predominantly in the Baltic States, Poland, Denmark, Germany, and in southern Sweden) and in adjacent areas and a large proportion of historic and new amber collections contains this "sea amber". A precise locality of origin therefore cannot be provided for Baltic amber pieces from historic collections that were developed in the Königsberg (Kaliningrad) and Danzig (Gdansk) areas during the 19th and early 20th centuries. This fact does, however, not affect the age estimate given above since the majority was initially embedded in these Eocene sediments (Standke 2008).

Repository of the fossils

The specimens described in this study are deposited in the Geoscientific Collections of the University of Göttingen, Germany (GZG), in the Museum für Naturkunde Berlin, Germany (MB), and in the Geological-Palaeontological Institute and Museum (CeNak) of the University of Hamburg (GPIH).

Preparation, microscopy and illustration

The amber pieces were slightly ground and polished manually using a series of wet silicon carbide papers [grit from FEPA P 600 (25.8 µm particle size) to 4,000 (5 µm particle size), Struers, Germany] to produce smooth surfaces for investigation. A fraction of a millimetre of amber was gradually removed from each amber piece, while frequently checking the preparation under a dissection microscope to ensure that the inclusions were not damaged.

Amber pieces, once removed from the anoxic sediments, deteriorate over time. This degradation results in darkening of the amber surface and crazing which is the development of networks of fine surface cracks (Figs 2E, 9A) that further extend towards the centre of the amber pieces (Bisulca *et al.* 2012). Some of the investigated historic amber specimens have undergone severe degradation (Fig. 2).

Two ashlar-shaped amber specimens (*Fungites hirtus* and *Calicium succini*) were originally embedded in dammar resin (an angiosperm resin from Southeast Asia) inside small glass chambers mounted on microscopic slides (Figs 2A, C). Oxidative damage of the dammar resin obviously started when the glue that was originally applied to fix the glass slide, glass frame, and cover slip degraded which then brought the resin in contact to air. This process obfuscated the view of the inclusions (Figs 2B, D). In addition, the thick glass cover slips and the layer of dammar resin caused too much light scattering for microscopic investigation and imaging of the amber inclusions. In order to allow state-of-the art documentation of the fungi, which were still perfectly preserved inside these amber specimens over a century after initial preparation, we removed the glass cover slip and then carefully removed the dammar resin using a scalpel. As the dammar resin is softer than the embedded amber, this process did not damage the historic amber specimens. The ashlar-shaped amber specimens were then further ground and polished until relevant structures were clearly visible under 200-fold magnification.

Some historic amber specimens that were not embedded in natural resins had heavily degraded and the light-scattering caused by the numerous surface cracks hindering the study of the inclusions (Fig. 2E). The fissured outer portions of these amber specimens were removed by careful grinding and polishing to ensure a clear view on the inclusions (compare Fig. 2E and Fig. 13).

Prepared amber specimens were mounted on a glass microscopic slide with the upper polished surface oriented horizontally. A drop of water was applied to the upper surface of the amber and

covered with a 0.06-0.08 mm thickness glass coverslip (Menzel Inc., Braunschweig) to reduce light scattering from fine surface scratches and to improve optical resolution.

The amber inclusions were studied under a Carl Zeiss Stereo Discovery V8 dissection microscope and under a Carl Zeiss AxioScope A1 compound microscope, equipped with Canon 5D digital cameras. In most instances, incident and transmitted light were used simultaneously. For an enhanced illustration of the three-dimensional inclusions, the light-microscopical images are digitally stacked photomicrographic composites from up to 80 individual focal planes using the software package Helicon Focus 6.2.2.

After investigation, fragile amber pieces were fully embedded in a high-grade epoxy (Epotec 301-2, Epoxy Technology) under vacuum (see Nascimbene and Silberstein 2000 for protocols) to ensure long-term preservation of the fossils.

REVISION OF CASPARY'S FUNGI

Here we provide amended descriptions of Caspary's fungi on the basis of original descriptions and illustrations and the six original specimens that we were able to locate. For five of the seven specimens that are lost we cite the original descriptions and compare them to the most likely conspecific fossils that have since been found from Baltic amber. These additional specimens show the observational acuity of Caspary and Klebs and allow understanding the morphology, reproduction and ecology of the fungi from the Baltic amber forest. However, we found no new fossil resembling the lost *Ramularia*-like inclusions. For convenience and clarity, we treat the fungal morphologies that we can firmly identify first, followed by taxa of uncertain systematic assignments; thus the order of the taxa here differs from the way they were originally presented in Caspary & Klebs (1907a, b). There are 13 morphologies but 14 numbers in plate 1 of Caspary & Klebs (1907b) (Fig. 1) since *Casparyotorula globulifera* was illustrated in two figures by Caspary & Klebs (1907b). We discuss the affiliations of the fossils and their substrates.

Phylum ASCOMYCOTA Cavalier-Smith, 1998

Subphylum PEZIZOMYCOTINA Eriksson & Winka, 1997

Class DOTHIDEOMYCETES Eriksson & Winka, 1997

Order CAPNODIALES Woronichin, 1925

Family METACAPNODIACEAE Hughes & Corlett in Hughes, 1972

Genus METACAPNODIUM Spegazzini, 1918

Metacapnodium succinum (Dörfelt, A. R. Schmidt & J. Wunderlich) Rikkinen, Dörfelt, A. R. Schmidt &Wunderlich, 2003

Figure 3

?1858 *Sphaerophorus moniliformis* Menge, p. 9, figs 1–2.

?1907a, b *Torula mengeanus* R. Klebs in Caspary & Klebs, p. 14, pl. 1, fig. 9.

2000 *Rosaria succina* Dörfelt et al., pp. 328–332, figs 1–8.

2003 *Metacapnodium succinum* (Dörfelt, A. R. Schmidt & J. Wunderlich) Rikkinen et al., p. 253 figs 1–7.

MycoBank. MB 373789.

Holotype. Senckenberg collection (Frankfurt am Main, Germany), SMF Be 526a (formerly Jörg Wunderlich Amber Collection, F70/BB/PL/CYA/CJW).

Other material. GZG.BST.24348.

Klebs' description of Torula mengeanus. Delicate fungus covering a *Thuites* twig. Branched filaments of globose to oblate cells of 8.5–11.4 µm diameter tightly appressed to the plant surface. Erect filaments of 11.4–51.1 µm length emerge and consist of 3–9 apically tapering cells.

Description of GZG.BST.24348. Sooty mould growing on a Cupressaceae twig fragment with affinities to the morphotaxon '*Thuites*' sensu Caspary (Fig. 3A) which, however, still needs revision. Hyphae brown, moniliform, branching and distally tapering (Fig. 3B, C). Cells widely barrelshaped or globose to subglobose, 4.5–18 µm long and 6–18 µm wide. Many hyphae bear brown, lageniform conidiophores 6–8 µm long and 3–4.5 µm wide (*Capnophialophora* conidial state) (Fig. 3D). Phialoconidia are not seen.

Remarks. Klebs described *Torula mengeanus* based on a delicate fungus on a *Thuites* twig from the amber collection of Dr Sommerfeld in Königsberg (Caspary & Klebs 1907a), but he did not provide

a collection number for this specimen. His description of apically tapering branched moniliform filaments suggests that he saw a sooty mould of the Metacapnodiaceae family, which are known from numerous Baltic amber pieces (see Schmidt et al. 2014).

We found a Cupressaceae twig fragment in amber piece GZG.BST.24348 of the historic Königsberg Amber Collection in Göttingen (Fig. 3). The label indicates that this piece was part of the former Sommerfeld collection. Klebs' drawing (pl. 1, fig. 9) and some portions of mycelia in amber specimen GZG.BST.24348 (Fig. 3B–C) appear to be very similar but this does not prove that these amber specimens are identical.

In any case, *Torula mengeanus* cannot be assigned to the extant genus *Torula*, but rather represents a sooty mould of the family Metacapnodiaceae (Capnodiales, Ascomycota), darkly pigmented fungi which typically derive their nutrition from honeydew excreted by aphids, scale-insects and other sap-feeding insects. Metacapnodialean sooty moulds have distinctive hyphae that can be confidently identified to the family level (Hughes 1976; Chomnunti et al. 2014).

Sooty moulds have been previously described from several amber deposits around the world (Rikkinen et al. 2003; Schmidt et al. 2014). Fossil specimens of *Metacapnodium* from Baltic and Bitterfeld ambers have recently been assigned to *Metacapnodium succinum* (see Rikkinen et al. 2003). However, the oldest description of a probable sooty mould fossil is *Sphaerophorus moniliformis* Menge, 1858. The holotype of this fungus is lost but based on the original description and illustration, Caspary & Klebs (1907a) concluded that it most likely to have been the same fungus as their *Torula mengeanus*.

Class LECANOROMYCETES Eriksson & Winka, 1997

Order CALICIALES Bessey, 1907

Family CALICIACEAE Chevallier, 1826

Genus CALICIUM Persoon, 1794

Calicium succini (Caspary) Rikkinen & A. R. Schmidt comb. nov.

Figure 4

1886 *Stilbum succini* Caspary, p. 8 (nomen dubium).

1907a, b *Stilbum succini* Caspary; Caspary & Klebs, p. 16, pl. 1, fig. 13.

1927 *Stilbites succini* (Caspary); Pia, 1927, p. 124, fig. 117.

MycoBank. MB 823683.

Basionym. *Stilbum succini* Caspary, 1886 (p. 8).

Holotype. MB.Pb.1979/838 (Thomas Amber Collection).

Description of the original specimen. Thallus crustose, episubstratic on bark fragment (Fig. 4A, B). Single ascoma rising from thallus, 480 µm high. Stipe 75–120 µm wide, widest at the base, surface smooth and epruinose. Capitulum lenticular to disc-shaped, 175 µm wide (Fig. 4C). Mazaedium well-developed but thin, protruding only slightly beyond excipulum edge. Ascospores one-septate, dark brown, ellipsoidal with a clear incision at septum, 7.5–11 x 4.5–5.5 µm.

Remarks. This fungus was described by Caspary (1886) as *Stilbum succini*. The extant basidiomycete *Stilbum vulgare* Tode, 1790 (Agaricostilbales, Pucciniomycotina) produces basidiospores on stalked basidiomata (Oberwinkler & Bandoni 1982; Bauer et al. 2006), which superficially resemble the structure preserved in amber. During the nineteenth and twentieth centuries numerous *Stilbella* Lindau, 1900 (in Engler & Prantl 1900) species and other ascomycete producing erect synnemata with slimy heads have also been named *Stilbum* Tode, 1790, and the generic term stilbum is sometimes used in reference to the synnema of such fungi (Seifert 1985; Kirk et al. 2008).

Our new analysis of the fossil revealed that it undoubtedly is a crustose lichen of the genus *Calicium* (Caliciaceae, Caliciales, Ascomycota), and the necessary new combination is proposed above.

Phylum, class, order and family INCERTAE SEDIS

Genus ACREMONITES Pia, 1927

Acremonites succineus (Caspary) Pia, 1927

Figure 5

1886 *Acremonium succineum* Caspary, p. 8 (nomen dubium).

1907a, b *Acremonium succineum* Caspary; Caspary & Klebs, p. 10, pl. 1, fig. 5 (nomen dubium).

1927 *Acremonites succineus* (Caspary) Pia, p. 122. MycoBank. MB 115027.

Holotype. Museum von Stantien und Becker no. 10; specimen apparently lost.

Original description. Caspary (1886) described this dark brown fungus from a leaf of *Widdringtonites oblongifolius* Göppert & Menge var. *longifolius* Caspary. Conidiophores are dark brown, often semi-translucent near the tip, straight and erect, 85.2–96.6 µm long and 4.2 µm wide. Conidia dark brown, often semi-translucent near the base, 23 µm long and 17 µm wide; the original description does not include any information on possible septation. The drawing in Caspary & Klebs (1907b pl. 1, fig. 5) does not reveal further distinguishing characters.

Description of closest available specimen. Amber specimen GZG.BST.24479 contains a conifer twig fragment with monomorphic spirally arranged needles, which resembles *Taxodium* sp. (Cupressaceae, Fig. 5A). A hyphomycete with stalk-like conidiophores and prominent, globular conidia is located on the degraded surface of the leaves (Fig. 5B, C). The conidiophores of this fungus are brown to dark brown, macronematous, straight, growing solitarily, 20–48 µm long (without light-coloured apex and conidium), 3–4.5 µm wide. The apex of a conidiophore is light-coloured or semi-translucent, 3–10 µm long and 3– 8 µm wide. In some cases the apex region is divided into two distinct, hyaline cells, the apical conidiogenous cell being long and slender, and the cell at the base being wider and much shorter. Each conidiophore bears a single globular to slightly ellipsoidal, light brown to dark brown conidium, 1-septate, and 9–12 µm in size (Fig. 5B, C). Only six conidiophores with a conidium still attached were found, and most of the conidiophores have their light-coloured apex region ruptured rhexolytically. No mycelium is present at the base of the conidiophores. In its overall morphology this hyphomycete is quite similar to Caspary's fungus, but smaller and with clearly septate conidia. In any case, it is the closest presently available analogue for *Acremonites succineus* (Caspary) Pia 1927.

Remarks. The type species of genus *Acremonium* Link, 1809 (Hypocreales, Ascomycota), *A. alternatum* Link, 1809, has hyaline, often slimy conidia borne in basipetal chains (Seifert et al. 2011). Caspary (1886) mentioned that *A. succineum* resembled *Acremonium fuscum* J. C. Schmidt, 1817, which was transferred to *Acremoniella* by Saccardo (1886) (as *Acremoniella fusca* (J. C. Schmidt) Saccardo). According to Seifert et al. (2011) the name *Acremoniella* is not valid and the correct name for that genus is *Harzia* Constantin, 1888. Caspary's *Acremonium succineum* differs from extant *Harzia* species in having unbranched, pigmented conidiophores rather than

sympodially branched, hyaline conidiophores. For these reasons the name *Acremonites succineus* (Caspary) Pia, 1927 seems to be the most appropriate name for the fossil (Pia 1927).

Acremonites succineus does not correspond with the current concept of either *Acremonium* or *Harzia* and, on the basis of its conidiophores and conidia, it more resembles some species of *Endophragmia* Duvernoy & Maire, 1920, *Acrogenospora* M. B. Ellis, 1971, and *Monotosporella* Hughes, 1958. Species of *Endophragmia* and *Acrogenospora* usually grow on dead wood, while *Monotosporella* species can also occur on decaying leaves and bark (Ellis 1971; Seifert et al. 2011).

Genus CASPARYOTORULA Rikkinen, A. R. Schmidt & Kettunen, 2015 in Kettunen et al. 2015

Casparyotorula globulifera (Casp.) Rikkinen, A. R. Schmidt & Kettunen in Kettunen et al., 2015

Figure 6

1886 Torula globulifera Caspary, p. 8 (nomen dubium).
1907a, b Torula globulifera Caspary; Caspary & Klebs, p. 12, pl. 1, figs 7, 8 (nomen dubium).
2015 Casparyotorula globulifera (Casp.) Rikkinen, A. R. Schmidt & Kettunen in Kettunen et al., p. 186; pl. 2, figs 1–14; pl. 6, figs 2–6.

MycoBank. MB 811954.

Holotype. MB.Pb.1979/696 (Künow Amber Collection no. 153).

Description of the original specimen. Colonies brown to dark brown, effuse (Fig. 6A). Vegetative hyphae hyaline to light brown, 1–3 µm wide, smooth. Secondary conidiogenous hyphae become more pigmented with age and have a rough surface ornamentation (Fig. 6E–F). Conidiogenous cells brown to dark brown, monoblastic or polyblastic, intercalary, terminal or integrated. Conidia moniliform and their detachment schizolytic. Mature conidia dark brown, in simple or branched chains, smooth, (23) 26–42 µm long and (4.5) 5.3–6.2 (7.0) µm wide, 7-septate, but often breaking into 3-septate units (Fig. 6B–D).

Remarks. Caspary (1886) described this fossil fungus in Baltic amber and assigned it to the extant anamorphic genus *Torula* (Persoon) Link, 1809. However, the fungus lacks conidiogenous cells

typical to modern *Torula* species, and therefore Kettunen et al. (2015) recently transferred it to the new fossil genus *Casparyotorula*. For more details on the morphology, condiogenesis, and affinities of the fungus, see Kettunen et al. (2015).

Casparyotorula heteromorpha (Casp.) Rikkinen, A. R. Schmidt & Kettunen, 2015 in Kettunen et al. 2015

Figure 7

1886 *Torula heteromorpha* Caspary, p. 8. 1907a, b
Torula heteromorpha Caspary; Caspary & Klebs, p. 14; pl. 1, fig. 10. 2015
Casparyotorula heteromorpha (Casp.) Rikkinen, A. R. Schmidt & Kettunen 2015 in Kettunen et al., p. 189; pl. 3, figs 1–13

MycoBank. MB 811955.

Holotype. MB.Pb 1979/636 (Künow Amber Collection no. 68).

Description of the original specimen. Colonies effuse. Vegetative hyphae hyaline to light brown, 1.5–3 µm wide, smooth. Conidiogenous hyphae 3–4.5 µm wide, becoming more pigmented with age and developing a rough surface ornamentation (Fig. 7A, B). Conidiogenous cells brown to dark brown, monoblastic or polyblastic, intercalary, terminal or integrated. Mature conidia dark brown, narrowly ellipsoidal, subcylindrical to obovate, in simple or branched chains, smooth, (6) 14–28 (40) µm long and 4–8 µm wide, predominately 3-septate, slightly constricted at the septa (Fig. 7C, D). Cells of conidia obpyriform or moniliform. Detachment of conidia schizolytic.

Remarks. *Casparyotorula heteromorpha* (originally named *Torula heteromorpha*) is the second toruloid fungus described by Caspary (1886) from Baltic amber. Both *Casparyotorula heteromorpha* and *C. globulifera* have since been found also from Bitterfeld amber. In the holotype of *C. heteromorpha* the substrate of the fungus is not preserved, but it is most likely that the fungus was epiphytic like *C. globulifera*. *Casparyotorula* species are relatively common in European Palaeogene ambers. Figure 7C and D show pieces of conidial chains of *C. heteromorpha*

that have started to germinate after being embedded in resin. It is possible that this fungus was able to grow on semiliquid or solidified resin. For more details on the morphology, conidiogenesis, and affinities of the fungus, see Kettunen et al. (2015).

Genus FUNGITES Hallier, 1860

Unidentified filamentous organism

Figure 8 1907a, b

Fungites capillaris Caspary & R. Klebs, p. 9, pl. 1, fig. 1.

MycoBank. MB 107498. Holotype. Museum von Stantien und Becker, no. 15702 (formerly Caspary's private collection no. 7); specimen apparently lost.

Original description. Caspary & Klebs (1907a, b) described *Fungites capillaris* as a mass of thin filamentous hyphae growing on a leaf of *Thuites succineus* Caspary & R. Klebs, 1907a. The hyphae measured 1.0–1.4 µm in diameter, with no spores visible.

Description of closest available specimen. The holotype of *Fungites capillaris* appears to have been lost. A large colony of filaments in a recently found amber specimen (Geoscientific Collections of the University of Göttingen, GZG.BST.21973 (formerly Jörg Wunderlich Amber Collection no. F158); Fig. 8) closely corresponds with the description and drawing of *Fungites capillaris* in Caspary & Klebs (1907a, b). The pale pillow-like structure is 12 mm in diameter and consists of delicate simple or sparsely branching filaments (Fig. 8A–D). The filaments are 1–5 µm wide (Fig. 8G, H) and in some places, rod-shaped cells of c. 1 µm diameter and 4–10 µm length inside a sheath are visible (Fig. 8H). However, most filaments are surrounded by bubbles which are often so abundant that they give the impression of forming a surrounding sheath of up to 40 µm diameter around the filaments (Fig. 8D–G). In some cases, such gas-filled spaces have become pyritized and are now brownish in colour. No spores or other reproductive structures are present, and the filamentous mass has been preserved on a degraded semi-translucent layer of plant tissue. The filaments do not seem to have been broken or stretched by the pull of flowing resin. Although the colony of filaments in the new amber specimen is considerably larger than those described and illustrated

by Caspary & Klebs (1907b, pl. 1, fig. 1), we propose that the new specimen is the closest presently available equivalent to the original specimen.

Remarks. The fossil genus *Fungites* was originally established by Ernst Hallier in 1860 for the fossil fungus *Fungites toeckianus* Hallier, 1860 (see also Hallier 1866). The name has since been used for miscellaneous, often fragmentary fossil remains of filamentous fungi that cannot be more accurately identified (Pia 1927).

Bacterial filaments and fungal mycelia are sometimes found growing inside resin before it solidifies (Schmidt & Dilcher 2007; Beimforde & Schmidt 2011). Based on growth pattern and general morphology we presume that the colony in the new amber specimen was produced by a filamentous prokaryote. *Leptothrix*-like sheathed bacteria have been previously described from Cretaceous European amber (Schmidt & Schäfer 2005; Saint Martin & Saint Martin 2017) but their sheaths are quite different from the sheath-like structure surrounding the filaments of the present specimen. The abundant preservation of minute gas bubbles around the filaments suggests that the colony was metabolically active and growing until the resin solidified.

In summary, as the holotype of *Fungites capillaris* is lost and this fossil species cannot be placed with certainty in any existing lineage, we suggest that it is best treated as a fossil of unknown affiliation.

Fungites hirtus Caspary & R. Klebs, 1907a, b

Figure 9

1907a, b *Fungites hirtus* Caspary & R. Klebs, p. 10, pl. 1, fig. 3.

MycoBank. MB 107499.

Holotype. MB.Pb.1979/614 (Künow Amber Collection no. 29).

Description of the holotype. Dark brown setae on an angiosperm leaf (Fig. 9A), setae multiseptate, 2–5 µm (1– 2 µm at the tip) wide and approximately 70–150 µm long with acute apices and

swollen bases up to 9 µm wide (Fig. 9B, C). In most cases the setae appear to grow from between plant cells (Fig. 9D, E).

Remarks. Considering the distribution of the fungus, it is most likely to have been a partially endophytic parasite that infected the angiosperm leaf when it was still alive. There is no thallus developed on the leaf surface, suggesting that the setae did not belong to an epiphyllous crustose lichen. Many extant ascomycetes produce similar setae, and without preserved reproductive structures it is impossible to assign the fossil with certainty to any specific modern group. The mesophyll of the leaf substrate is badly degraded, and there are faecal pellets associated with leaf openings, indicating that arthropods had been feeding on the leaf prior to its preservation.

Fungites macrochaetus Caspary & R. Klebs 1907a, b

Figure 10 1907a, b

Fungites macrochaetus Caspary & R. Klebs, p. 10, pl. 1, fig. 4.

MycoBank. MB 107500.

Holotype. GZG.BST.24490, formerly Bernstein-Museum von Stantien und Becker no. 15703. (Casparysche Privatsammlung (C.P.S.) no. 67).

Description of the holotype. Dark brown conidiophores rising from the surface of a small, stalked angiosperm fruit (Fig. 10A, B). Conidiophores macronematous, straight or flexuous, growing solitarily or in tufts or loose fascicles, (90) 300–500 (600) µm long and 5–14 µm wide (3–8 µm at the tip), proliferating precurrently and sometimes branching (Fig. 10C, D). Conidiogenous cells nodelike, polyblastic, integrated, at first terminal, but later also intercalary as the conidiophore grows in height (Fig. 10E, F). Production of conidia appears synchronous. Conidia simple, ellipsoidal to ovoid, light brown to brown, 1– 2.5 µm wide and 3–5 µm long (Fig. 10G, H). Conidia do not appear to have been produced in chains, or at least no chains are seen even though detached conidia are preserved in the amber matrix. No vegetative hyphae visible.

Remarks. Caspary & Klebs (1907a, b) mentioned that no spores were visible in the condiophores. However, we were able to detect numerous minute conidia, both attached to the conidiophores and free in the surrounding amber matrix (Fig. 10E, G, H).

Fungites macrochaetus resembles extant species of the genus *Gonatobotryum* Saccardo, 1880, but the preserved conidiophores appear to be quite aged making this identification very uncertain. It is most likely that the fungus was a parasite or an opportunistic saprophyte. There are no signs of a host response in the fruit, and it is unclear whether the fungus had already infected the fruit when it was still attached to the plant.

Fungites pullus Caspary & R. Klebs 1907a, b

Figure 11 1907a, b

Fungites pullus Caspary & R. Klebs, p. 9, pl. 1, fig. 2.

MycoBank. MB 107501.

Holotype. Museum von Stantien und Becker no. 15703; specimen apparently lost.

Original description. Caspary & Klebs (1907a, b) described Fungites pullus as a filamentous fungus forming anastomosing networks of brown hyphae on a leaf of *Thuites* Sternberg, 1823. The anastomosing network of hyphae (2.07– 3.03 µm wide) bore erect hyphae 33.1–45.5 µm long and 3.03–4 µm wide. The authors mention that this fungus is quite common in Baltic amber and that similar hyphae had been seen also growing on other conifer leaves.

Description of closest available specimen. The holotype of *Fungites pullus* is lost, but a fungus preserved on the abaxial side of an angiosperm leaf in amber specimen GZG.BST.24340 appears to be a very close analogue (Fig. 11). The leaf was originally described as being of coniferous origin (Kettunen et al. 2015). In a recent study, Sadowski et al. (2017a) assigned leaf inclusions similar to GZG.BST.24340 to the angiosperm morphotaxon *Dicotylophyllum*; however, their identity is still a matter of debate. The adaxial side of leaf GZG.BST.24340 is partly covered by the hyphomycete *Casparyotorula globulifera* (Caspary) Rikkinen, A. R. Schmidt & Kettunen, 2015 (Kettunen et al.

2015; see Fig. 6E–F). Networks of septate brown hyphae of 2–4.5 µm width grew on the abaxial leaf surface tracing the borders of epidermal cells, branching and forming anastomoses in a similar manner to those illustrated by Caspary & Klebs (1907b) (Fig. 11A, B). From these hyphal networks rise erect conidiophores 18–120 µm long and 3–6 µm wide, some with multiseptate conidia developing at the apex (Fig. 11C, D). The conidia are up to 15 µm long and 4 µm wide.

Remarks. It remains unclear if the fungi from the adaxial (see Fig. 6E–F) and abaxial leaf side (Fig. 11) are conspecific or if two anamorphic fungi are present on the leaf inside amber specimen GZG.BST.24340. Morphologically similar conidiophores are produced by many different ascomycetes (see e.g. Seifert et al. 2011), but exact comparisons are impossible as details of conidiogenesis cannot be seen in the fossil.

Genus GONATOBOTRYTITES Pia, 1927

Gonatobotrytites primigenius (Caspary, 1886) Pia, 1927

Figure 12

1886 *Gonatobotrys primigenia* Caspary, p. 8 (nomen dubium).
1907a, b *Gonatobotrys primigenia* Caspary; Caspary & Klebs, p. 11, pl. 1, fig. 6 (nomen dubium).
1927 *Gonatobotrytites primigenius* (Caspary, 1886); Pia, p. 122, fig. 111.

MycoBank. MB 115070.

Holotype. Museum für Naturkunde zu Berlin (Künow Amber Collection no. 138); specimen apparently lost.

Original description. The lost holotype was a brown hyphomycete with 73.8–198.8 µm long conidiophores that are 4.2– 7.1 µm wide. Conidia were described as ellipsoidal, about 1.9 µm long and half as wide (Caspary & Klebs 1907a). The fungus grew on an unidentified angiosperm flower.

Description of closest available specimen. A newly found filamentous fungus in amber specimen GZG.BST.24367 (Fig. 12) is very similar to *Gonatobotrytites primigenius*, and differs from it only by

its slightly larger conidia. Also, this fungus grew on the flower of an angiosperm (Fig. 12A). The partly superficial mycelium is brown and composed of 3–6 µm wide hyphae. The upright conidiophores are brown to light brown, macronematous, straight or flexuous, growing solitarily or in tufts or loose fascicles, (60) 150–240 (480) µm long and 4–14 µm wide at the base and 3–9 µm wide at the apex (Fig. 12B, C). Conidiophore apices are often more lightly pigmented than the basal parts. Conidiophores are nodose with conidiogenous ampullae (Fig. 12D–G). The conidiogenous cells are brown to light brown, polyblastic, integrated, first terminal, later intercalary, percurrent, globose to subglobose. The oldest conidia seem to be at the base of the ampulla with younger ones developing apically (Fig. 12G). Conidia are pale, ellipsoidal to globular, 3– 4 µm long and 1–2 µm wide. Several detached conidia are preserved in the amber matrix (Fig. 12H).

Remarks. We were unable to locate the type specimen of *Gonatobotrytites primigenius* in the amber collection of the Museum für Naturkunde Berlin, although the specimen was listed when the Künow Amber Collection was obtained by the museum.

Dörfelt & Schmidt (2007) discussed the systematic placement of the fossil and emphasized its close similarity with extant species of *Gonatobotryum*. Caspary & Klebs (1907a) mentioned that *Gonatobotrytites primigenius* was similar to *Gonatobotrys fusca* Saccardo, 1877, which had already at that time been transferred to *Gonatobotryum* as the type species (*Gonatobotryum fuscum* (Saccardo) Saccardo, 1880) of the new genus. Dörfelt & Schmidt (2007) described another similar fossil fungus from Baltic amber, *Gonatobotryum piceae* Dörfelt & Schmidt, 2007, growing on a conifer seedling. For a detailed comparison of the two fossil species and *Gonatobotryum fuscum*, see Dörfelt & Schmidt (2007).

Conidiophores of the *Gonatobotryum*-like fungus in amber specimen GZG.BST.24367 are somewhat longer and wider than those of *Gonatobotrytites primigenius* and *Gonatobotryum piceae*, and the mature conidia of *G. piceae* are larger. Otherwise our fungus is morphologically similar to these two other fossil species. It has smaller conidia than the extant *Gonatobotryum fuscum* and shorter conidiophores, but in other respects the fossil is very similar to modern *Gonatobotryum* species, which grow on other fungi, wood or galls (Seifert et al. 2011). It is probable that the fossil fungus was also a saprophyte growing on a decaying flower.

Ramulariites oblongisporus (Caspary) Pia, 1927 1886

Ramularia oblongispora Caspary, p. 8. (nomen dubium). 1907a, b
Ramularia oblongispora Caspary; Caspary & Klebs, p. 15, pl. 1, fig. 11 (nomen dubium). 1927
Ramulariites oblongisporus (Caspary); Pia, p. 122.

MycoBank. MB 499762.

Holotype. Museum von Stantien und Becker no. 15705; specimen apparently lost.

Original description. Caspary & Klebs (1907a, b) described and illustrated two filamentous microfungi in the genus Ramularia Unger, 1833. *Ramulariites oblongisporus* (originally named *Ramularia oblongispora*) grew on an angiosperm fruit and was described as producing colourless filaments 45.4–51.1 µm long and 2.8–4.2 µm wide. Detached conidia were described as 2.8 µm wide and two to three times that in length. According to the drawing the filaments seem to consist of narrow conidiogenous hyphae and chains of somewhat wider and hyaline, ellipsoidal conidia.

No specimen number was provided for the second *Ramularia* fossil described by Caspary & Klebs (1907a, b, p. 16, pl. 1, fig. 12) which grew on stamens of an angiosperm flower. Colonies of the fungus consisted of 3–6 dark brown to black conidiophores 74–284 µm long and 7.6– 8.5 µm wide. Some conidiophores had developed narrowly ellipsoidal, 8.5–11.4 µm long conidia in acropetal chains. The detachment of apical conidial cells was also mentioned by Caspary & Klebs (1907a).

Remarks. We could not find any similar specimen from Baltic amber. The extant genus *Ramularia* has over 300 species. Most of them are plant pathogens but also saprotrophic and mycophilic species are known. Some species are well-known pathogens of important crop plants. The genus as presently delimited seems to be polyphyletic (Seifert et al. 2011; Videira et al. 2016). Typical *Ramularia* species have hyaline, unbranched or sparingly branched conidiophores with hyaline conidia that are borne singly or in unbranched or branched acropetal chains, and the secession of conidia is schizolytic. Conidiogenous cells are hyaline with distinct thickened, darkened scars. However, there are also several morphologically similar genera and the systematic relationships between these have not yet been elucidated. In many cases distinguishing *Ramularia* species from

those of morphologically similar genera may be impossible without molecular methods (Videira et al. 2016). For these reasons the name *Ramulariites oblongisporus* (Caspary) Pia 1927 seems to be the most appropriate name for the (lost) fossil (Pia 1927).

Unidentified possible fruticose lichen

Figure 13

1907a, b Cetraria sp. Caspary & Klebs, p. 18, pl. 1, fig. 14.

Material. GZG.BST.24489.

Description of the original specimen. This amber specimen contains a branch of a fruticose lichen that was assigned to the extant genus *Cetraria* Acharius, 1803 by Caspary (1886). The main branch is approximately 13 mm high, and at its widest around 1 mm wide. Smaller branches are 200–800 µm wide, with the tips often forked (Fig. 13).

Remarks. Despite being visually impressive, the fossil does not reveal other diagnostic features in addition to the overall habit and branching pattern. The fossil is a hollow cast and its surface is completely fissured (Fig. 13); even submerging the fossil in water in vacuum did not make the fissures disappear. On the basis of the preserved features it is not possible to assign the fossil to any existing lichen lineage confidently. Podetial branches of some *Stereocaulon* Hoffmann, 1796 and Cladonia P. Browne, 1756 species (Lecanorales, Lecanoromycetes) are of comparable size and can show a similar branching pattern, but without seeing the surface structure, even the possibility of this fossil being a plant root cannot be totally dismissed (Kaasalainen et al. 2015).

NEWER DISCOVERIES OF FOSSIL FUNGI FROM BALTIC AMBER

The following fossils are new fungal morphologies that have been recently found from Baltic amber and further demonstrate the diversity of microfungi from Baltic amber.

Phylum ASCOMYCOTA Cavalier-Smith, 1998

Subphylum PEZIZOMYCOTINA Eriksson & Winka, 1997

Class DOTHIDEOMYCETES Eriksson & Winka, 1997

Order cf. CAPNODIALES Woronichin, 1925

Family, genus and species INCERTAE SEDIS

Sooty mould ascomata

Figure 14

Material. GZG.BST.24619.

Description. The amber piece contains a small fragment of a conifer branch ('*Thuites*' sensu Caspary, Cupressaceae, Caspary & Klebs 1907a) (Fig. 14A) that has several different microfungi growing on it. Most noticeable are two superficial ascomata, of which one is intact, and the other one partially ruptured (Fig. 14B). Both ascomata are only partially attached to the branch, which is probably due to the pull of the resin flow when the branch was embedded in resin. The intact ascoma is 100 µm in diameter, dark brown and more or less globular, with multicellular, sometimes branching setae; the ruptured ascoma is 120 µm in diameter. Setae dark brown to brown, 77–92.5 µm long and 2–8 µm wide, tapering towards the apex and terminating in a hyaline, thin-walled apical cell. Cells cushion-like, mostly globular, 7.5–12 µm in diameter. No ascospores are preserved. The ascomata are closely associated with different types of hyphae, some of which are identical to the vegetative hyphae of extant Metacapnodiaceae. These hyphae are moniliform, branching and distally tapering, with cells 6– 12 µm in diameter. There are also straight, long hyphae with less conspicuously rounded cells relatively near the ascomata, with cells 9–18 µm long and 6–18 µm wide.

Remarks. The relatively well preserved ascomata were most probably produced by a sooty mould. However, without preserved ascospores their more precise identification is not possible. Mature ascomata of extant Metacapnodiaceae tend to be considerably larger than those of the fossil, and they are also often more clearly immersed in the substrate (Corlett et al. 1973; Hughes et al. 2012; Chomnunti et al. 2014). Some species in the family Capnodiaceae (Saccardo) Höhnel *ex* Theissen, 1915 (Capnodiales) have superficial ascomata that are very similar to fossil fungi (Chomnunti et al. 2014). It thus seems likely that the ascomata were produced by a capnodilean sooty mould.

Amber specimen GZG.BST.24658 (Fig. 15B, C) contains the original specimen of *Chamaecyparis casparyi* R. Klebs (Cupressaceae; Caspary & Klebs 1907a, pl. 17, figs 84, 84a–d), which has Metacapnodiaceae hyphae that had produced conidia (*Capnophialophora* or *Capnobotrys* conidial states). The majority of sooty mould hyphae in this specimen grew in the small cavities that are formed between the leaves, most presumably because of favourable moisture conditions and due to the fact that honeydew easily accumulates in these microhabitats.

Class and Order INCERTAE SEDIS

Family TRICHOPELTINACEAE (Theissen & P. Sydow) Batista et al., 1958

Genus and species INCERTAE SEDIS

Figure 15

Material. GZG.BST.24658 (Fig. 15B, C), GZG.BST.24611 (Fig. 15A, D), GZG.BST.24470, GZG.BST.24592, GZG.BST. 24346; GPIH 4950 (Carsten Gröhn Amber Collection 2678).

Description. Several pieces of Baltic amber contain fossils of a fungus with a flat, thin, superficial and irregularly lobed thallus (Fig. 15A, B). Thalli up to 800 x 600 µm in size. Cells rectangular to cylindrical, dark brown to brown, 4.5–11 µm long and 2–4 µm wide (Fig. 15C–D). Thyriothecia visible as darkened, more or less globular areas, but no ostioles or released ascospores are visible.

Remarks. These epiphytic fungi seem to be common on Cupressaceae leaves in Baltic amber, and specimen GZG.BST.24346 also contains a similar fungus on an angiosperm leaf (*Dicotylophyllum* sp.; for details see Sadowski et al. 2017a). Fossils of epiphytic fungi with similar thallus morphologies have been previously described from several locations around the world (e.g. Cookson 1947; Dilcher 1965; Reynolds & Dilcher 1984; Sherwood-Pike & Grey 1988; Bannister et al. 2016; Conran et al. 2016). Many of these fossils have been assigned to the order Microthyriales G. Arnaud, 1918, which contains several predominately tropical or subtropical genera. Our fossils, however, more resemble extant fungi of the family Trichopeltinaceae (Theissen & P. Sydow) Batista, Costa & Ciferri, 1958 (Dothideomycetes). The thyriothecia of these fungi develop inside the flattened thallus. Extant species are mainly foliar epiphytes growing on plant leaves, and the group is widely distributed around the world. Colonies form darkened or black areas on plant

surfaces, and the thallus shapes of *Trichopeltina* Theissen, 1914a and *Trichopeltella* Höhnel, 1910 species are similar to thalli of the fossils. Extant *Trichopeltina* and *Brefeldiella* Spegazzini, 1889 species produce thin thalli consisting of radially arranged cylindrical to cuboid cells, with thyriothecia developing inside thallus tissue. These genera typify Trichopeltineae Theissen & Sydow, 1917 and Brefeldiineae Theissen & Sydow, 1917, the two subfamilies of Trichopeltinaceae, which was originally named Trichopeltaceae Theiss, 1914a (Theissen & Sydow 1917; Hongsanan et al. 2014). Species of *Brefeldiella* tend to produce rounded thalli whereas thalli in *Trichopeltina* are more linear or 'root'-like (Hongsanan et al. 2014). Also species of the genus *Trichopeltis* Spegazzini, 1889, which was recently transferred to *Trichothyrium* Spegazzini, 1889 (Trichothyriaceae Theissen, 1914b) by Wu et al. (2011), have a similar thallus morphology to that of the fossils. The exact affinities of both families remain unclear (Wu et al. 2011; Hongsanan et al. 2014).

In summary, based on thallus structure, the fossils most closely resemble extant Trichopeltina species (Trichopeltinaceae). However, as no ascospores were found their exact affinities remains uncertain. A similar fungus was recently described from New Zealand and placed in the fossil genus Trichopeltinites Cookson, 1947 (Bannister et al. 2016).

Class, order, family and species INCERTAE SEDIS

Gonatobotryum-like fungus

Figure 16

Material. GZG.BST.21950.

Description. Growing on branch and fruits of the dwarf mistletoe *Arceuthobium viscoides* (Göppert & Berendt, 1845) Sadowski et al., 2017b (Fig. 16A). Small filamentous fungus with numerous upright straight or flexuous conidiophores 100–160 (320) µm long and 2–11 µm wide, often with swollen bases. Conidiophores macronematous, growing solitarily, in tufts or in loose fascicles, pale brown to brown and smooth, in many cases shrivelled during desiccation (Fig. 16B). Conidiogenous cells forming nodes along the conidiophores, nodes first terminal, but then becoming intercalary as the fungus grows (Fig. 16C–E). Conidia produced synchronously. Conidiogenous cells polyblastic and integrated, brown, 7.5–9 µm wide and 6–7.5 µm high, distinctly roughened by minute conidial scars (Fig. 16E). Mature, detached conidia pale brown,

non-septate, ellipsoidal to ovoid, 4– 10 µm long and 2–4.5 µm wide. Young conidia still attached to the conidiophores pale, often teardropshaped or with an elongated base (Fig. 16C, D). In two cases conidia had formed a short chain that was still attached to the conidiophore (Fig. 16C), and also some detached conidia were attached to each other in short chains.

Remarks. A variety of plant pathogenic fungi have been reported from extant *Arceuthobium* species, among them *Colletotrichum gloeosporioides* (Penzig) Penzig & Saccardo in Saccardo, 1884, *Cylindrocarpon gillii* (D. E. Ellis) J. A. Muir, 1973, and *Alternaria alternata* (Fries) Keissler, 1912 (Hawksworth & Geils 1996). However, none of these species are similar to the fossil fungus, which more resembles modern species of *Gonatobotrys* Corda, 1839 (the anamorph of *Melanospora* Corda, 1837; see Reblova et al. 2016) and *Gonatobotryum*, which have not been reported from dwarf mistletoes. *Gonatobotrys* includes three widely distributed extant species, mainly growing parasitically on other fungi, but also on litter, and they form conidia in acropetal chains in a similar manner as the fossil. *Gonatobotryum* includes four species that grow on other fungi or plants in Europe and North America (Seifert et al. 2011).

The dwarf mistletoe branch was described originally by Sadowski et al. (2017b). The branch is partially covered by spider web, and it seems likely that the small branch became detached and fell on the web before getting entrapped by resin. While parts of the branch are quite degraded, in some parts the leaves are very well preserved. No signs of a host response by the plant is visible, indicating that the fungus was most likely to have been an opportunistic saphrophyte that infected the mistletoe when it was at least weakened if not dead, but still attached to its host.

Class, order, family, genus and species INCERTAE SEDIS

Fungi producing multiseptate conidia on upright conidiophores

Figures 17, 18

Material. GZG.BST.24470 and GZG.BST.24619.

Description. In addition to the *Trichopeltina*-like fungus described above, one of the amber specimens (GZG.BST.24470) contains a small dematiaceous hyphomycete with erect, brown to dark brown conidiophores (Fig. 17A), colonizing a twig fragment of '*Thuites*' sensu Caspary

(Cupressaceae; Caspary & Klebs 1907a). Conidiophores 15–36 µm long and 2.5–4 µm wide, usually widened at the base (Fig. 17B). Conidiogenous cells integrated, terminal. Conidia cylindrical to oblong-elliptical, at least 1- to 2-septate, brown to dark brown, 9–17 µm long and 3–4.5 µm wide (Fig. 17C).

The light brown conidia on some conidiophores appear immature and were still developing when the fungus was embedded in resin. Some young conidia seem to develop from the detachment sites of older conidia which, on the other hand, sometimes seem also to have had the ability to rupture rhexolytically into two.

Besides sooty moulds, the Cupressaceae twig fragment ('*Thuites*' sensu Caspary, Caspary & Klebs, 1907a) preserved in GZG.BST.24619 also contains a darkly-pigmented hyphomycete with erect, brown to dark brown conidiophores and multiseptate conidia (Fig. 18A). Mycelium both superficial and immersed into substrate, consisting of brown 3–6 µm wide hyphae. Conidiophores upright, 49–75.5 µm long and 4.5–8 µm wide, with widened bases, appearing desiccated and brittle, with most conidia detached. Conidia multiseptate (up to at least 9-septate), brown to dark brown, cylindrical, 15– 67 µm long and 7.5–12 µm wide (Fig. 18B). Detachment appears to have been schizolytic. Apical regions of conidia and conidiophores lighter in colour.

Remarks. The two dematiaceous hyphomycetes described above are quite minute and with few identifiable characters. They differ from each other in several respects, but their affinities to modern genera are difficult if not impossible to determine. Many morphologically similar species are found in several genera including *Sporidesmium* Link, 1809 (sensu lato) and *Penzigomyces* Subramanian, 1992.

DISCUSSION

The original descriptions of fossil fungi from Baltic amber by Caspary & Klebs (1907a) contain remarkably precise and accurate measurements and descriptions. While the drawings of the fungi (Fig. 1) are not quite as detailed as the drawings of bryophytes and vascular plants in the atlas volume by Caspary & Klebs (1907b), together with the descriptions and our newly discovered specimens they allow us to understand the morphologies of specimens that have since been lost. Some fossil fungi have been utilized to study the evolution of extant fungal groups by using the

fossils for calibrating molecular phylogenies (e.g. Beimforde et al. 2014). Well-preserved and reliably identifiable fossils are valuable in estimating the divergence times of fungal lineages. In this context we can conclude that only two of Caspary's fossil fungi, *Metacapnodium succinum* and *Calicium succini*, can be used as minimum age constraints in molecular phylogenetic studies. Both specimens are exquisitely preserved, and their generic placements are clear and unambiguous.

The holotype of *Torula mengeanus* (Caspary & Klebs 1907a) is probably lost but is most likely to have been identical to the sooty mould *Metacapnodium succinum*, a common fungus of the Baltic amber forest (see Rikkinen et al. 2003, Schmidt et al. 2014). The overall morphology of *Calicium succini* (Caspary's *Stilbum succini*) including the single ascoma, the well-developed spore mass (mazaedium), one-septate ascospores, and the stipe, capitulum, mazaedium and ascospores of the fossil correspond exactly with those of several extant *Calicium* species (Tibell 1999). Another fossil *Calicium* has been found from Baltic amber (Rikkinen 2003), and this fossil has been used as a minimum age constraint for the genus *Calicium* and the family Caliciaceae in dating studies (Prieto & Wedin 2013, 2017; Beimforde et al. 2014).

Species of the extant genus *Torula* produce one-celled, dark or subhyaline moniliform conidia in typical 'toruloid' chains (Crane 2001; Seifert et al. 2011). Toruloid microfungi are frequently found in European amber and Caspary had already described two species (*Torula globulifera* and *T. heteromorpha*) from Baltic amber. The systematic position of these fossils remains unclear but they are not closely related to extant species of *Torula* (Kettunen et al. 2015). While over 400 species have been attributed to the genus over the years, Torula sensu stricto may actually only have less than ten species (Crane 2001; Seifert et al. 2011). Kettunen et al. (2015) established the genus *Casparyotorula* to accommodate the two species described by Caspary and also described a third species, *C. arnoldii*, from Bitterfeld amber.

Caspary's description of *Gonatobotrys primigenia* implies that the lost fossil was very similar to species in the modern genus *Gonatobotryum*. Additionally, there are two new fossil specimens described in this paper that confirm the presence of *Gonatobotryum*-like fungi in Baltic amber. Caspary's *Fungites macrochaetus* also resembles extant *Gonatobotryum* species, but the definite assignment is not possible since the fossil is missing many important characters like the chains of conidia.

Furthermore, we are certain that the fungi described by Caspary as *Acremonium* succineum, *Ramularia oblongispora* and *Ramularia* sp. do not belong to these extant genera, and we believe that the filamentous organism described as *Fungites capillaris* may have been a prokaryote and

not a fungus. *Fungites pullus* and *Fungites hirtus* are fossil ascomycetes of uncertain affinity and should remain in this fossil genus.

Caspary's classic specimens together with our new findings highlight the presence of epiphytic microfungi in Baltic amber belonging to Ascomycota (Subkingdom Dikarya). Microfungi are important in modern ecosystems as parasites, pathogens and decomposers, and wellpreserved fossil fungi associated to their substrates clearly demonstrate that they had a similar role in the past. In the early Eocene, much of central Europe was covered by dense tropical forests. This is also the traditional conception of the Baltic amber forest, but this view has recently been challenged by studies based on amber inclusions of vascular plants (Kohlman-Adamska 2001; Sadowski et al. 2017a). The morphological adaptations observed in the fossil lichens also suggest that the forest was humid but at least partly well-illuminated, and most probably temperate (Kaasalainen et al. 2017).

The sooty moulds probably got their nutrition from honeydew and did not actively harm their host plants. However, sometimes sooty mould colonies can cover leaf surfaces and thus interfere with the host plant's photosynthesis (Perez et al. 2009). Caspary's *Fungites hirtus* may have been an active parasite growing mostly inside the host plant's leaf. The other fossil fungi were probably saprophytes growing on dead or dying plant parts. With fossils of epiphyllic fungi it is often impossible to differentiate between parasitic and saprophytic lifestyles, especially if no evidence of host responses has been preserved.

The fungi described and discussed in this paper demonstrate a wide variety of fungal morphologies and ecologies from the 'Baltic amber forest'. Our re-examination of historical specimens led to significant changes in the interpretation and assignment of individual fossils, and provided new information about morphology and reproduction that was not documented when the fossils were first studied and described. This also underlines the importance of following best practice when using fungal fossils as minimum age constraints in molecular phylogenetic studies. Whenever possible, the original fossil specimens should be re-investigated in order to justify their phylogenetic placement (Kaasalainen et al. 2015).

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TABLES

TABLE 1. Caspary's fungi from Baltic amber: previous names and suggested affinities (Caspary and Klebs 1907*a*). MB: Museum für Naturkunde zu Berlin, GZG: Geoscientific Collections of the University of Göttingen. The numbers in brackets after some GZG numbers refer to original labelling of the Königsberg amber collection.

Illustration number and fossil names	**Historic specimen**	**Affiliation**	**Current taxonomic treatment**	**Closest available specimen**
1. *Fungites capillaris*	Lost	Prokaryota	Unidentified prokaryote	Jörg Wunderlich Amber Collection, no. F158
2. *Fungites pullus*	Lost	Ascomycota	*Fungites pullus*	GZG.BST.2 4340 (G4.511)
3. *Fungites hirtus*	MB 1979/614	Ascomycota	*Fungites hirtus*	
4. *Fungites macrochaetus*	GZG.BST.24490 (Casp. 86)	Ascomycota	*Fungites macrochaetus*	
5. *Acremonium succineum*	Lost	Ascomycota	*Acremonites succineus*	GZG.BST.24479 (NF 26A)
6. *Gonatobotrys primigenia*	Lost	Ascomycota	*Gonatobotryum primigenium*	GZG.BST.24367 (G5398)
7. and 8. *Torula globulifera*	MB 1979/696	Ascomycota	*Casparyotorula globulifera*	
9. *Torula mengeanus*	Probably lost	Ascomycota, Dothideomycetes, Capnodiales, Metacapnodiaceae	*Metacapnodium succinum*	GZG.BST.24348 (Casp 24 P)
10. *Torula heteromorpha*	MB 1979/636	Ascomycota	*Casparyotorula heteromorpha*	
11. *Ramularia oblongispora*	Lost	Ascomycota	*Ramulariites oblongispora*	none

TABLE 2. New fossil fungi from Baltic amber. GPIH, Geological-Palaeontological Institute and Museum (CeNak) of the University of Hamburg; GZG, Geoscientific Collections of the University of Göttingen. The numbers in brackets after some GZG numbers refer to original labelling of the Königsberg amber collection.

Fossil	**Affiliation**	**Specimen number(s)**
Gonatobotryum-like fungus	cf. *Gonatobotryum*	GZG.BST.21950 (Hoffeins 1422-2)
Trichopeltina-like fungus	cf. *Trichopeltina*	GZG.BST.24658 (G15), GZG.BST.24611 (B583), GZG.BST.24470 (Casp 38), GPIH 4950 (Carsten Gröhn Amber Collection 2678), GZG.BST.24592 (4B107), GZG.BST.24346 (G4507)
Unidentified hyphomycetes	Ascomycota	GZG.BST.24470 (Casp 38), GZG.BST 24619 (G59)
Sooty mould ascomata	cf. Capnodiales	GZG.BST.24619 (G59)

FIGURES

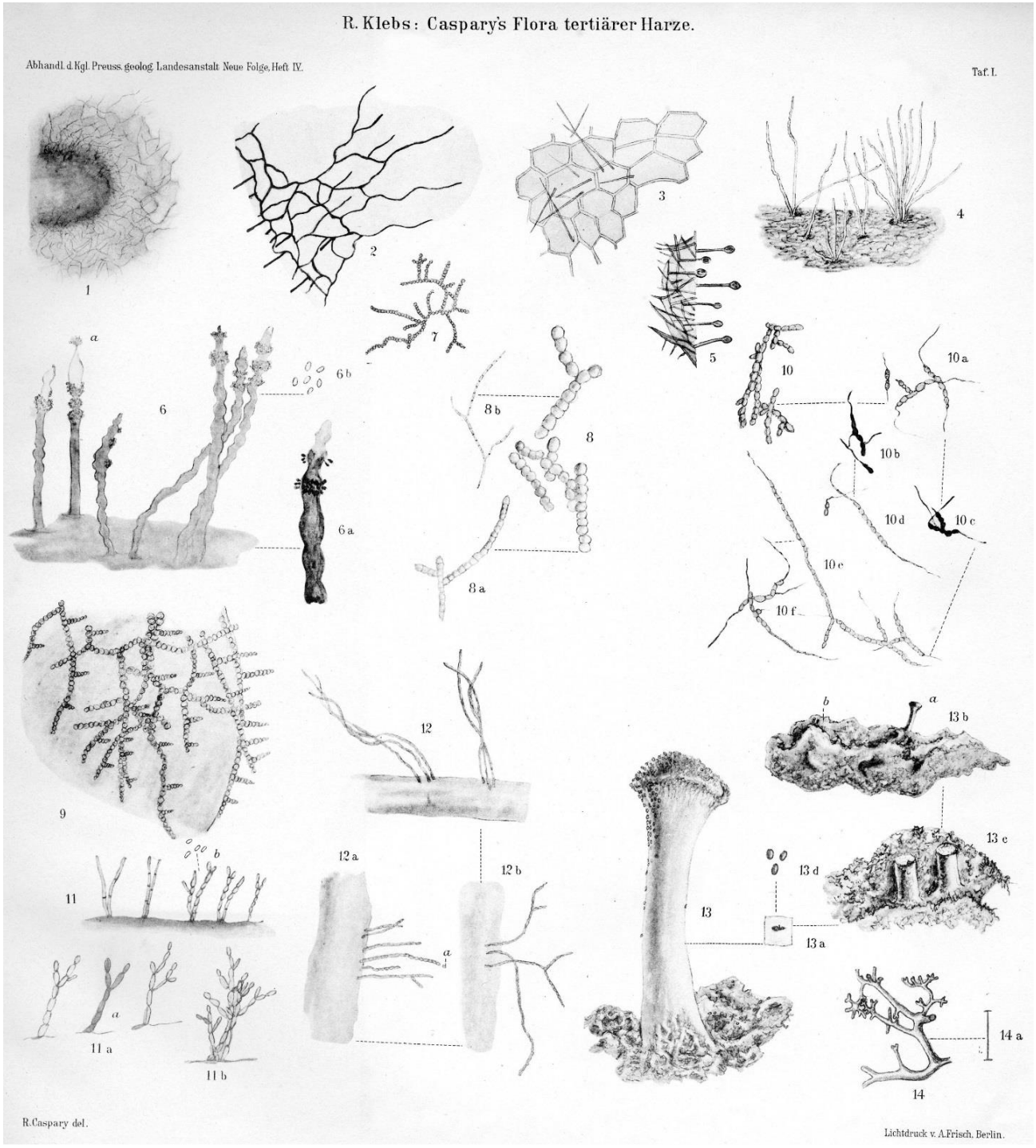

FIGURE 1. Reproduction of plate I of the atlas volume by Caspary & Klebs (1907b). See Table 1 for fossil names corresponding to illustrations 1–14.

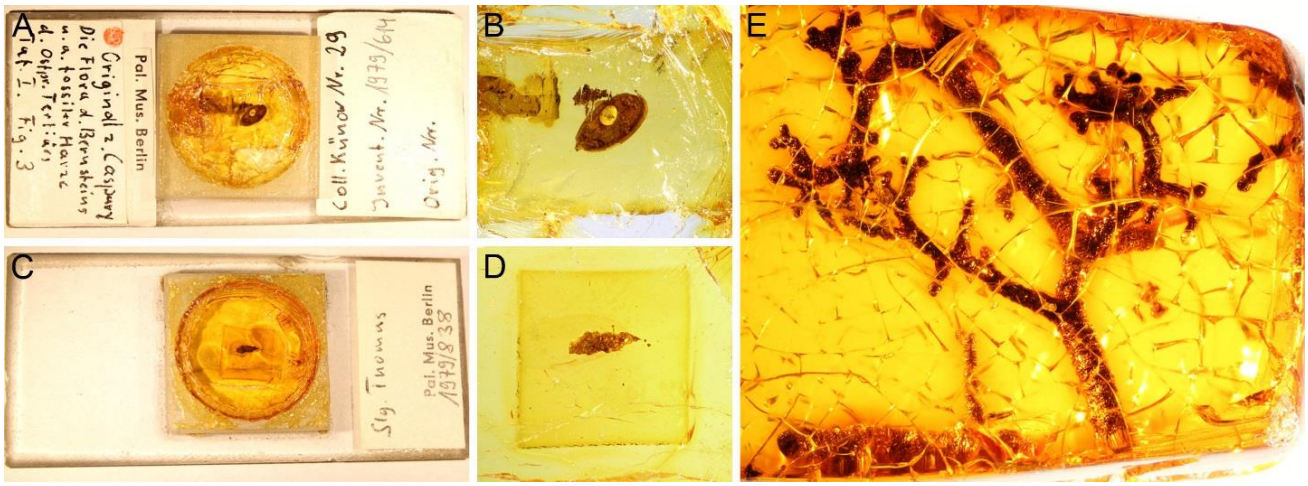

FIGURE 2. Examples of deterioration of historic amber preparations. A–B, original microscopic slide containing a leaf with *Fungites hirtus* before preparation (MB.Pb.1979/614, Künow Amber Collection no. 29). C-D, original microscopic slide containing *Calicium succini* (originally *Stilbum succini*) before preparation (MB.Pb.1979/838, Thomas Amber Collection). E, amber specimen containing a lichen (originally *Cetraria* sp.) before preparation (GZG.BST 24489).

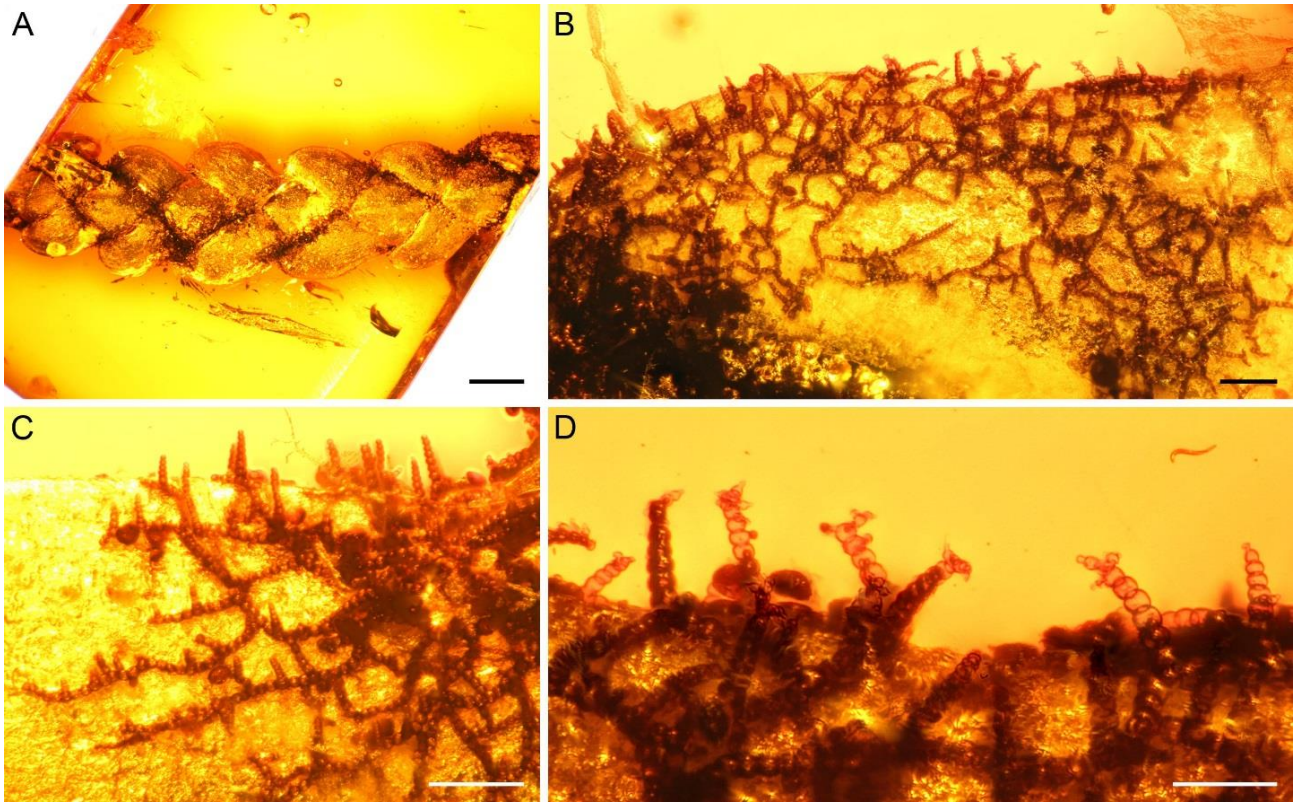

FIGURE 3. *Metacapnodium succinum* (GZG.BST.24348). A, overview of the conifer twig, the dark areas indicate mycelia. B–C, branched moniliform hyphae at the edge of the leaves. D, hyphae with *Capnophialophora* conidial states. Scale bars represent: 1 mm (A); 100 µm (B–C); 50 µm (D).

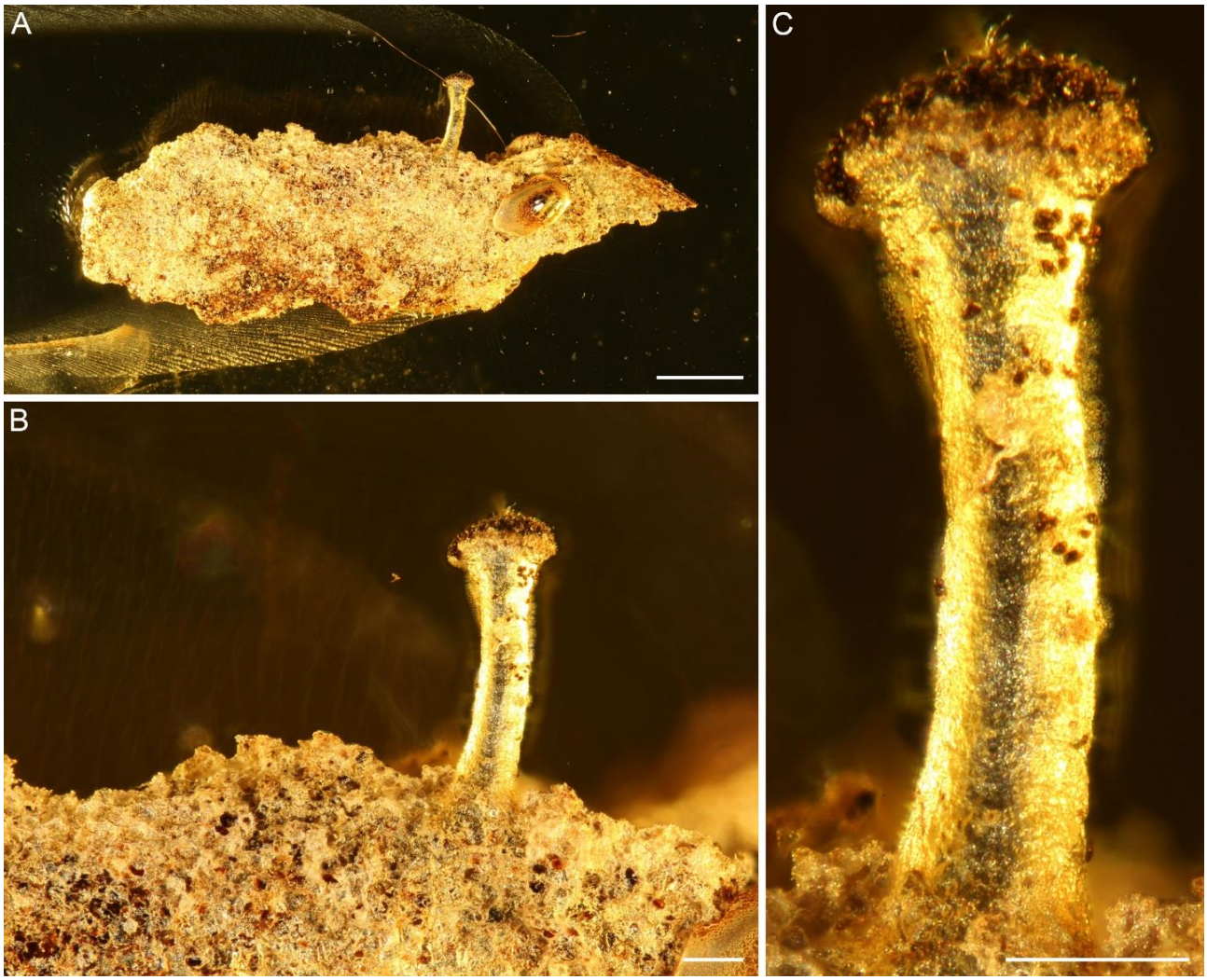

FIGURE 4. Holotype of *Calicium succini* (MB.Pb.1979/838; Thomas Amber Collection, no number). A, overview of the substrate with a single ascoma. B, ascoma with surrounding crustose thallus. C, stipe and the capitulum. Two-celled ascospores are best visible attached to the stipe. Scale bars represent: 500 µm (A); 100 µm (B–C).

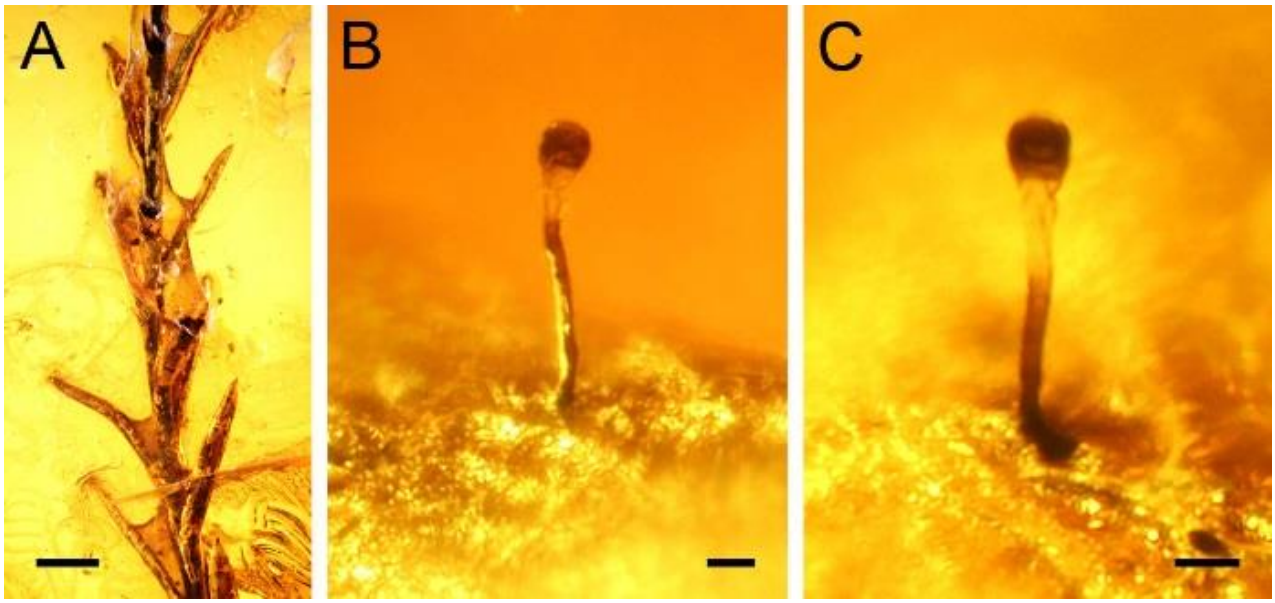

FIGURE 5. Unidentified hyphomycete resembling *Acremonites succineus* on a conifer twig (GZG.BST.24479). A, overview of the conifer twig. B–C, hyphomycete with upright conidiophores and globose, septate conidia. Scale bars represent: 1 mm (A); 10 µm (B–C).

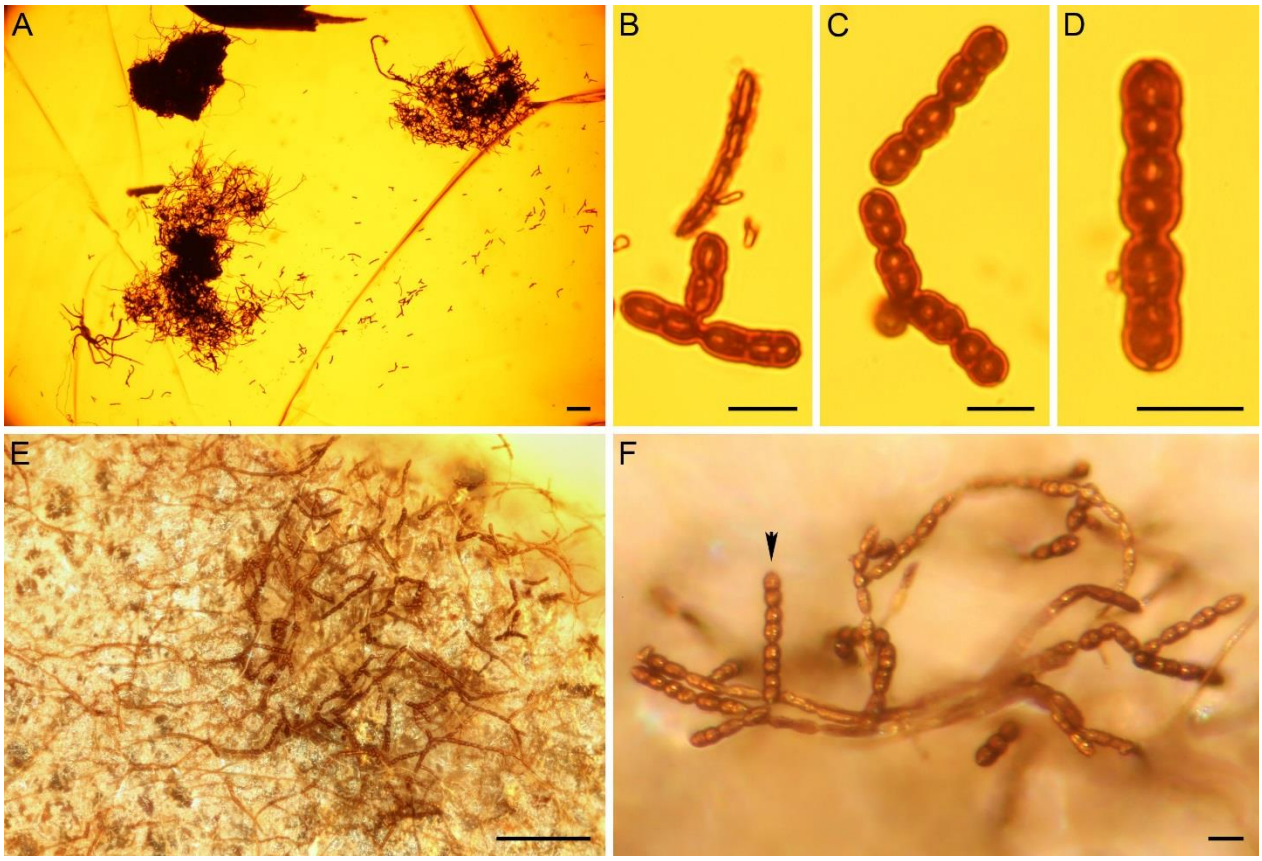

FIGURE 6. *Casparyotorula globulifera* from amber specimen MB.Pb.1979/696 (Künow Amber Collection no. 153) containing the holotype (A–D) and from amber specimen GZG.BST.24340 containing a leaf with fungi (E–F). A, two fragments of aerial mycelium and numerous detached conidia. B, fragment of hypha (top) and fragment of a branched conidial chain (down). C, two 7-septate phragmoconidia. D, single 7-septate phragmoconidium. E, hyphae and conidial chains at the edge of the angiosperm leaf. F, branched conidial chains; the arrowhead points to a single 7-septate phragmoconidium. Scale bars represent: 100 µm (A, E), 10 µm (B–D, F).

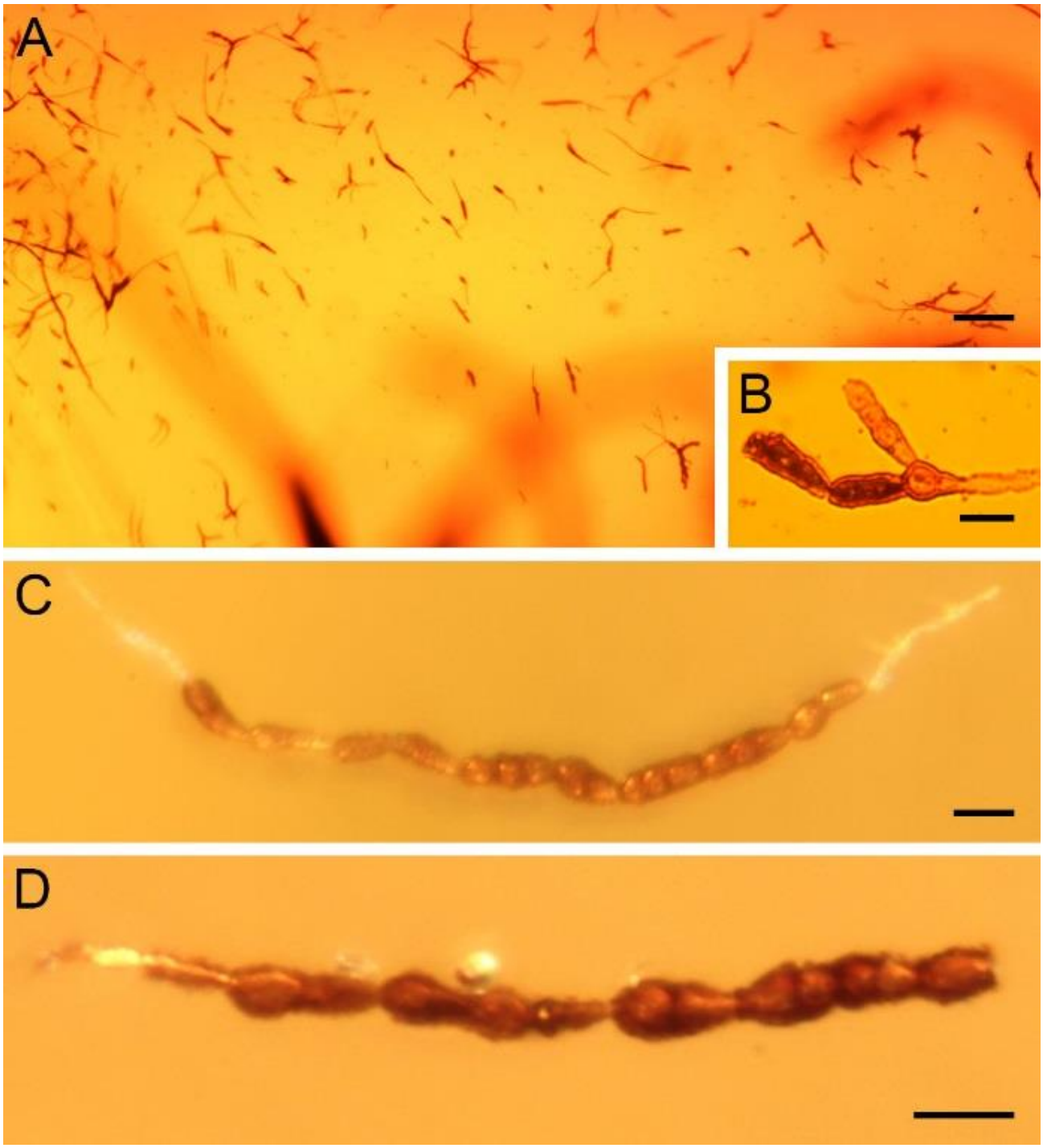

FIGURE 7. *Casparyotorula heteromorpha* from amber specimen MB.Pb 1979/636 (K€unow Amber Collection no. 68) containing the holotype (A–B) and from amber specimen GPIH 4949 (Carsten Gröhn Amber Collection 3628) (C–D). A, numerous fragments of conidial chains. B, holotype. C–D, germinating conidial chains. Scale bars represent: 100 µm (A); 10 µm (B–D).

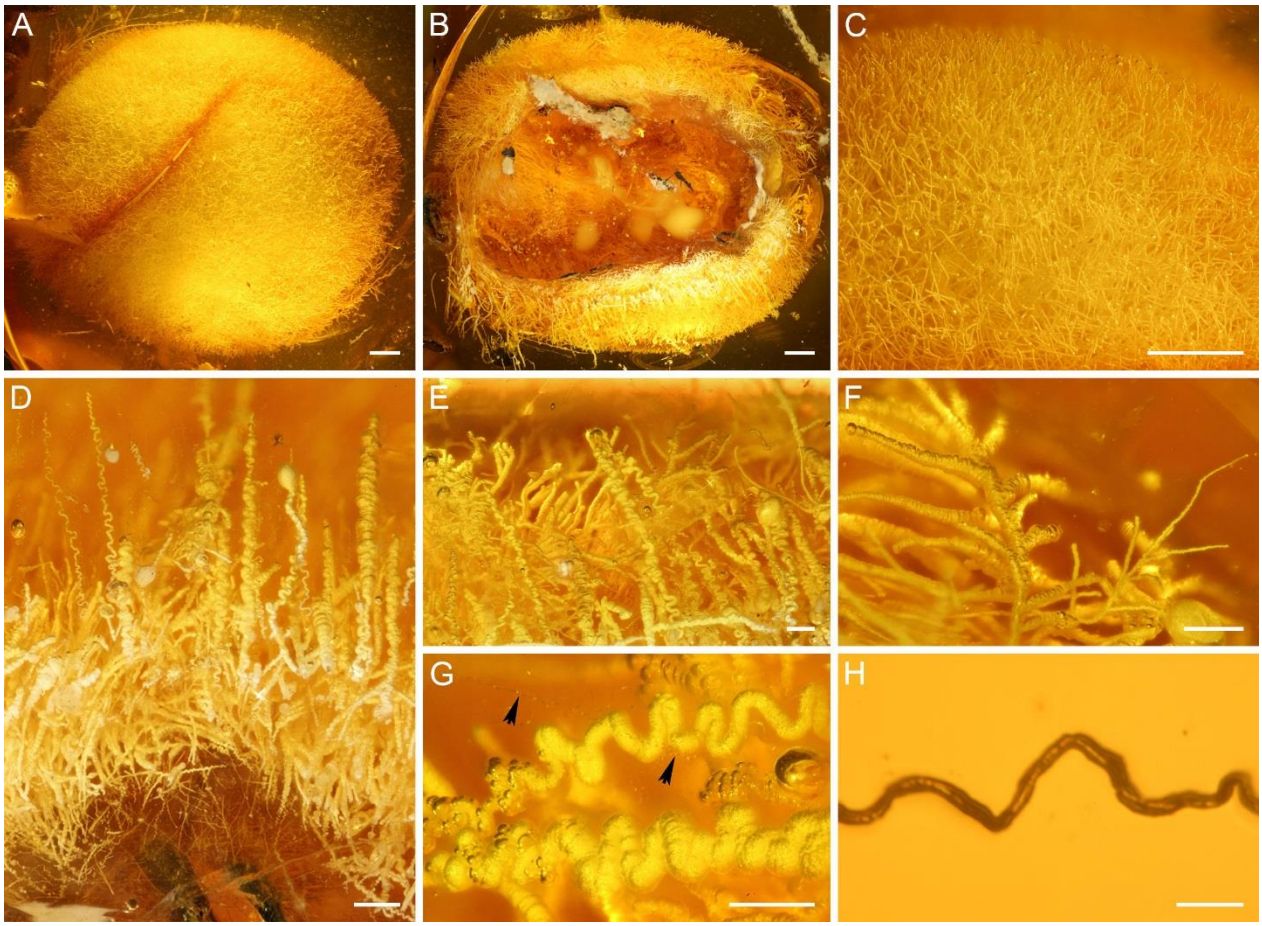

FIGURE 8. Filamentous organism resembling *Fungites capillaris* (GZG.BST.21973). A–C, overviews of the colony. D–F, sheathed filaments that are covered by numerous bubbles. G, filaments that are differently covered by gas bubbles, the arrowheads mark a filament that is not surrounded by bubbles. H, a close-up of a sheathed filament without surrounding bubbles; several rod-shaped cells are visible in the interior. Scale bars represent: 1 mm (A–C); 200 µm (D–G); 20 µm (H).

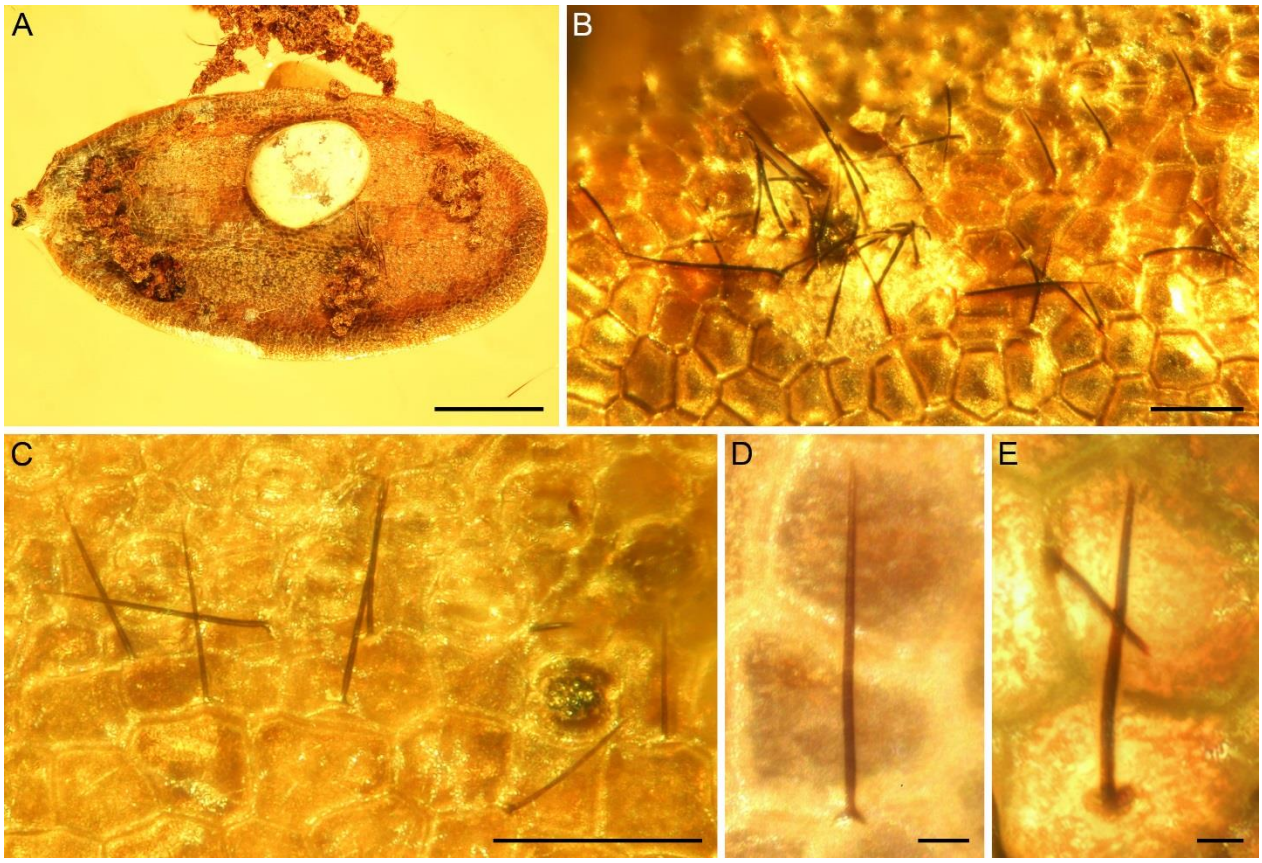

FIGURE 9. *Fungites hirtus* (MB.Pb.1979/614; K€unow Amber Collection no. 29). A, angiosperm leaf that served as the substrate; the arrowheads indicate the clusters of setae shown in (B) and (C). B–C, upright setae. D–E, details of setae growing on and from between the leaf epidermal cells; two septa are indicated by arrowheads. Scale bars represent: 1 mm (A); 100 µm (B–C); 10 µm (D–E).

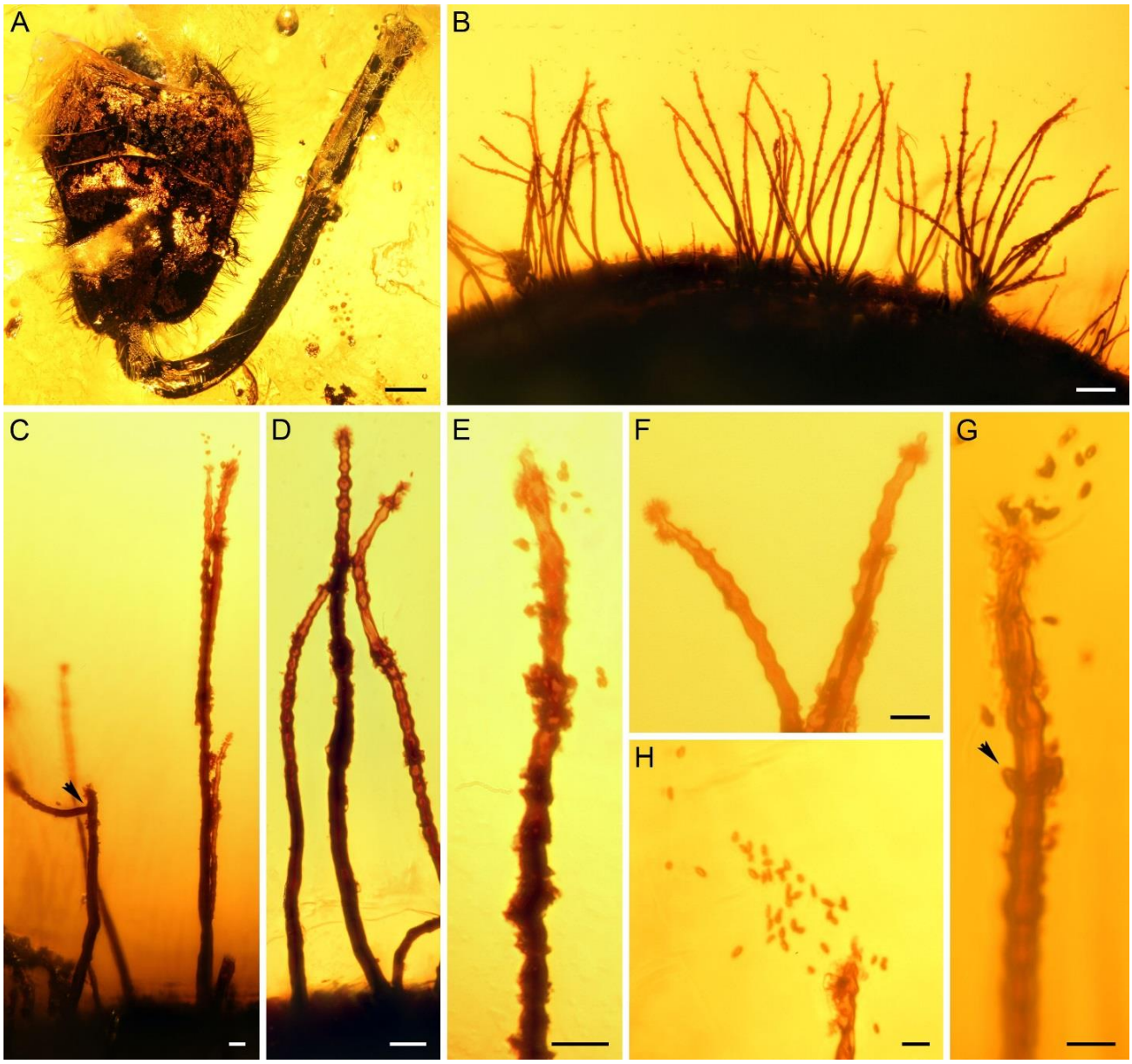

FIGURE 10. *Fungites macrochaetus* (GZG.BST.24490). A, stalked fruit with numberous conidiophores. B, overview of a group of conidiophores. C, conidiophores; the arrowhead marks a branching example. D–F, close-ups of the conidiophores showing nodose conidiogenous cells. G, sporulating conidiophore; the arrowhead points to an attached conidium. H, detached conidia. Scale bars represent: 1 mm (A); 100 µm (B); 20 µm (C–H).

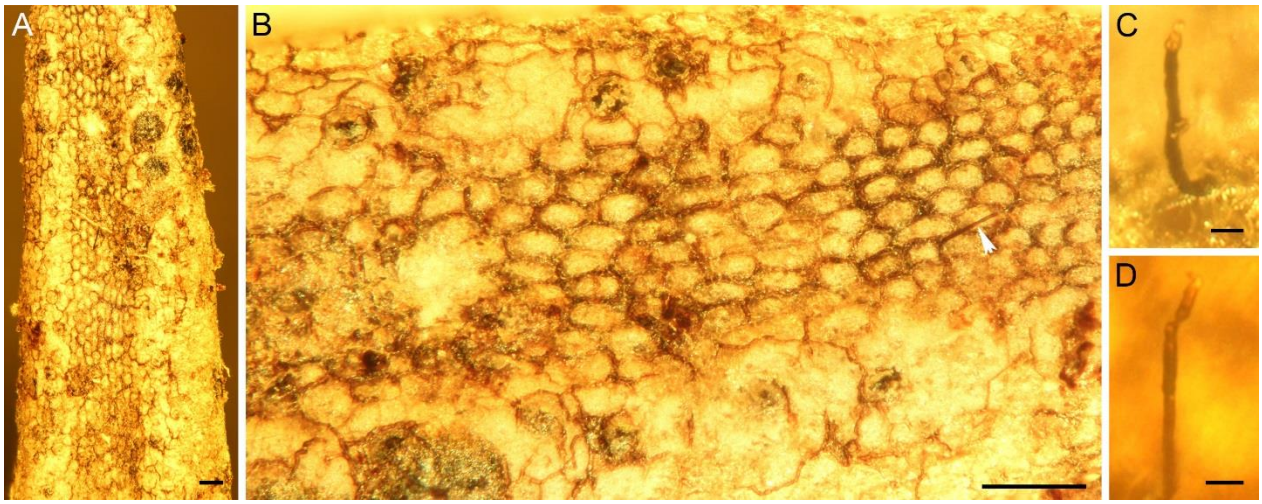

FIGURE 11. Fungus, probably conspecific with *Fungites pullus* (GZG.BST.24340). A–B, hyphal network on the abaxial side of an angiosperm leaf; the arrowhead points to an upright conidiophore. C–D, conidiophores with conidia. Scale bars represent: 100 mm (A–B); 10 µm (C–D).

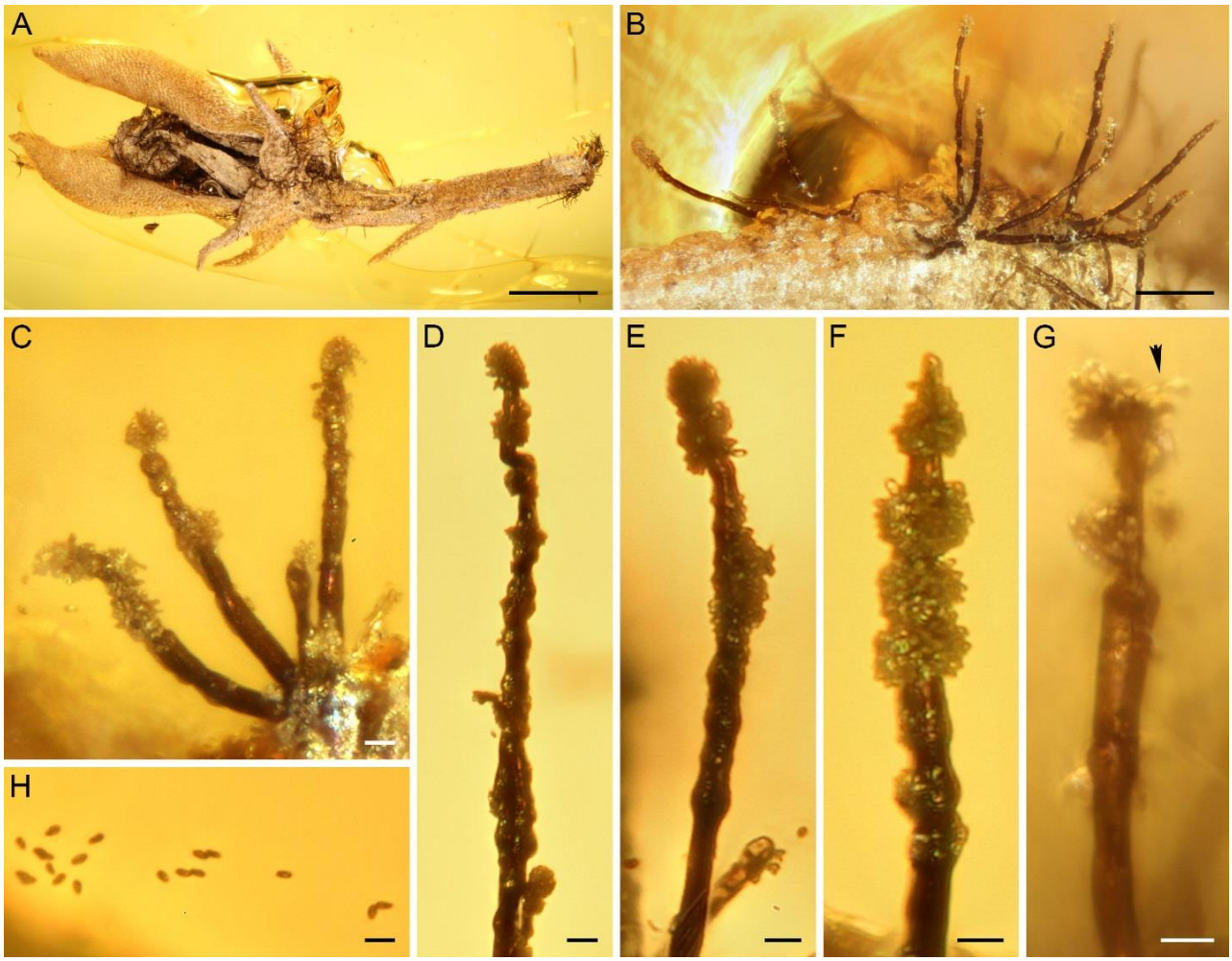

FIGURE 12. Fungus, probably conspecific with *Gonatobotrytites primigenius* (GZG.BST.24367). A, overview of the flower with scattered conidiophores. B, group of the conidiophores. C–G, dark conidiophores with pale conidia attached; the arrowhead in G points to two attached conidia. H, detached conidia in the amber matrix. Scale bars represent: 1 mm (A); 100 µm (B); 10 µm (C–H).

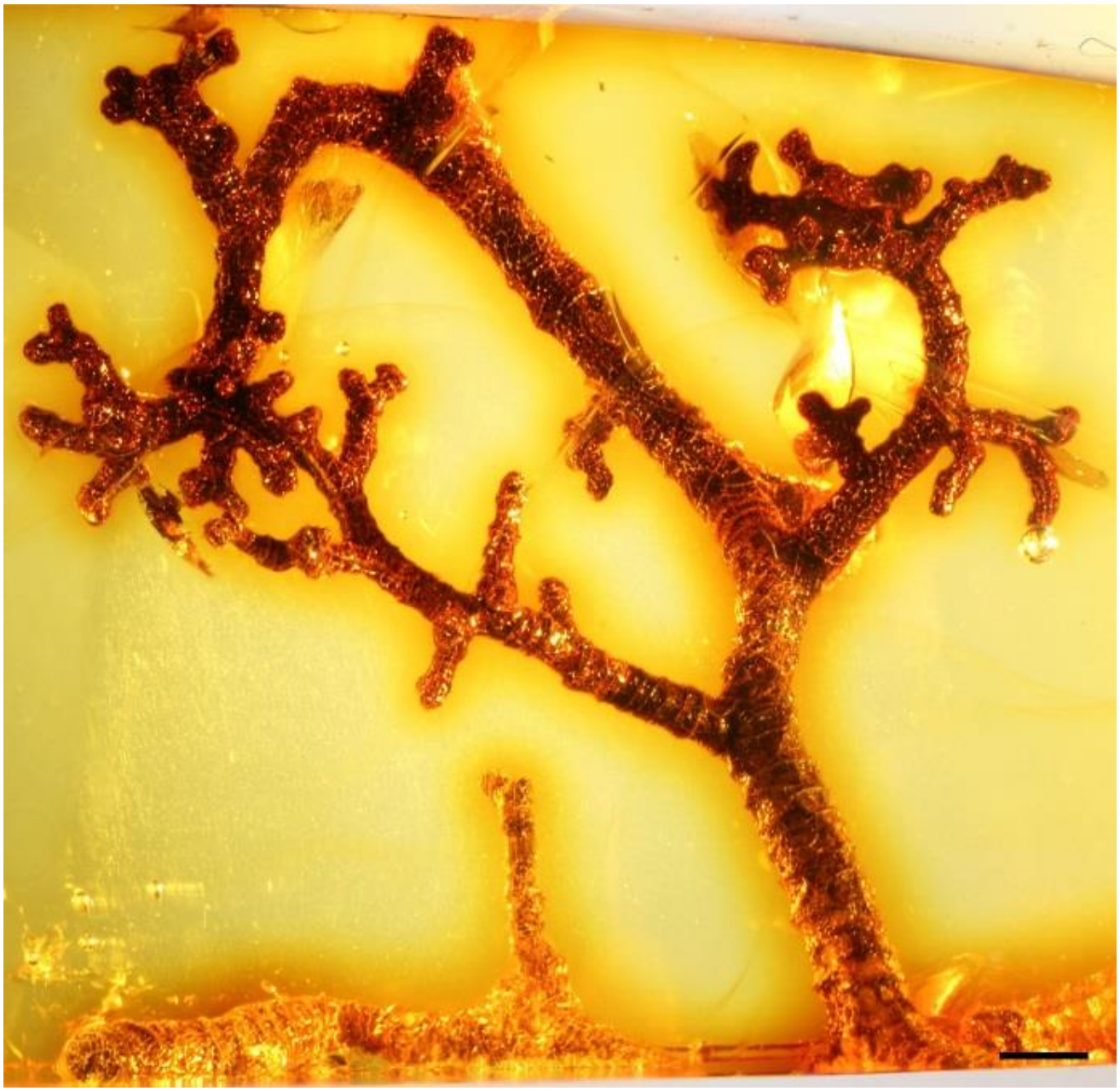

FIGURE 13. Unidentified and degraded fruticose lichen (GZG.BST.24489). Scale bar represents 1 mm.

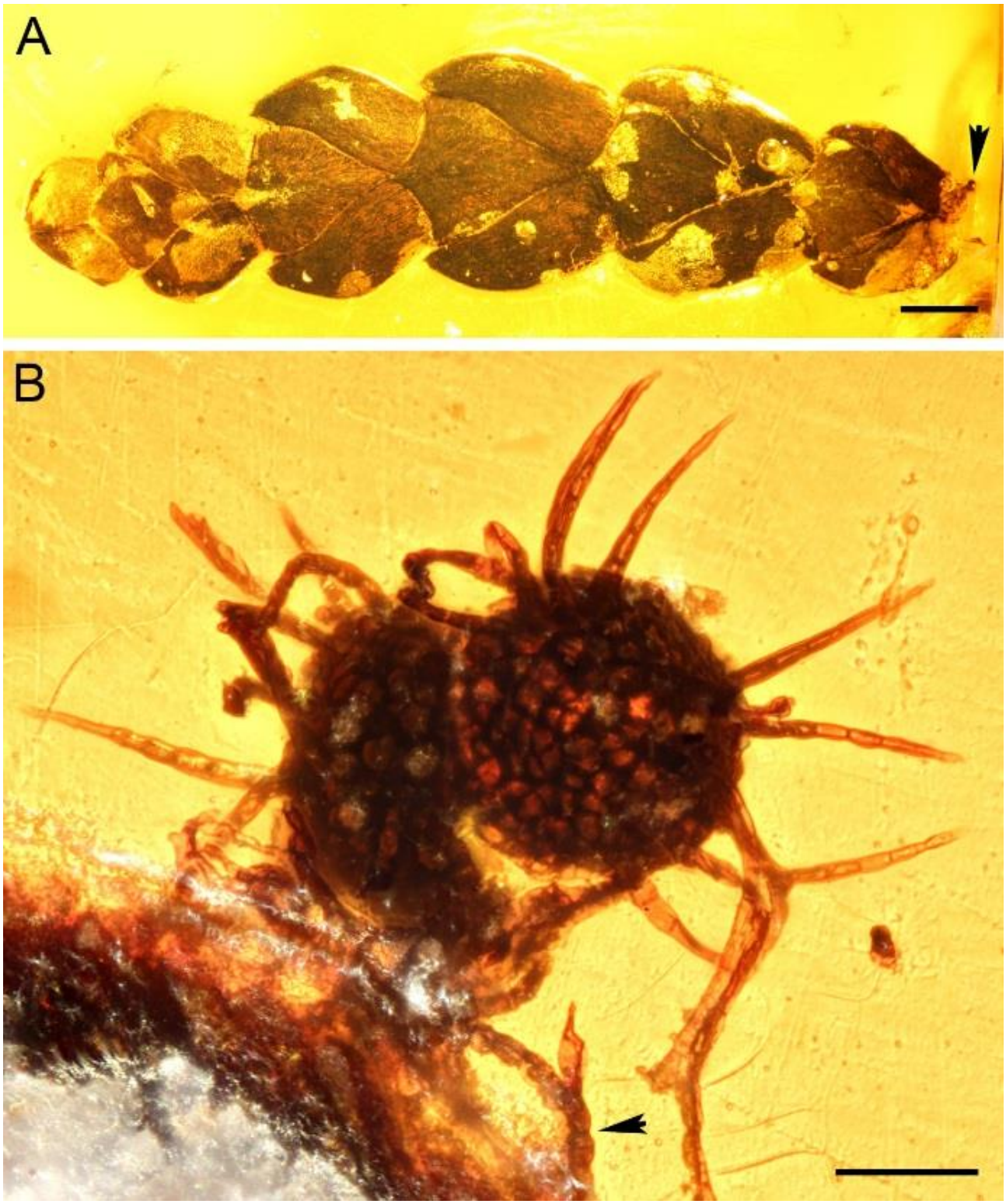

FIGURE 14. Sooty mould ascomata on a conifer branch (GZG.BST.24619). A, overview of the conifer branch; the arrowhead indicates location of the ascomata. B, two ascomata; the arrowhead marks vegetative hyphae of sooty moulds attached to the ascomata. Scale bars represent: 1 mm (A); 50 µm (B).

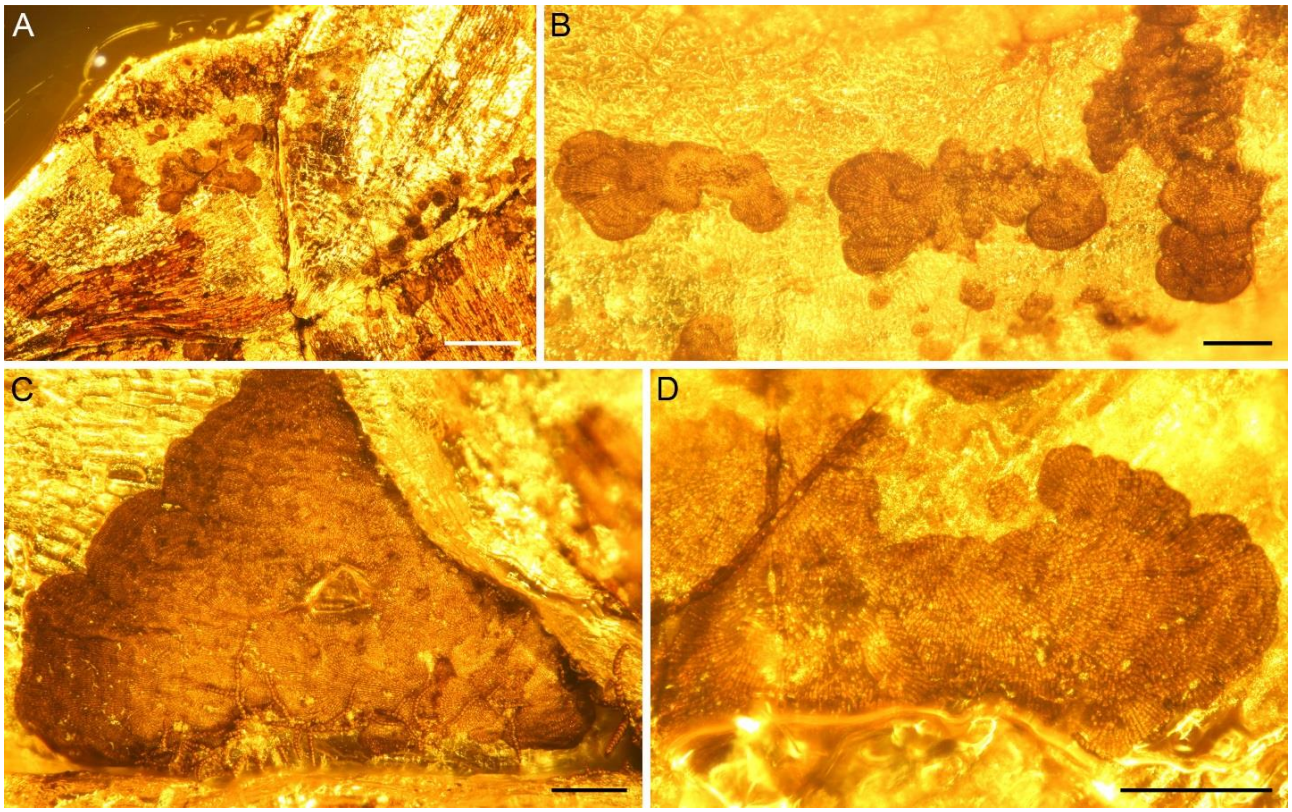

FIGURE 15. *Trichopeltina*-like fungi from amber specimens GZG.BST.24611 (A, D) and GZG.BST.24658 (B–C). A, overview of flat thalli growing on conifer leaves. B–D, detail of the thalli showing the growth pattern and rectangular cells; C also shows the association with moniliform hyphae of sooty moulds (filamentous structures towards base of micrograph). Scale bars represent: 500 µm (A); 100 µm (B–D).

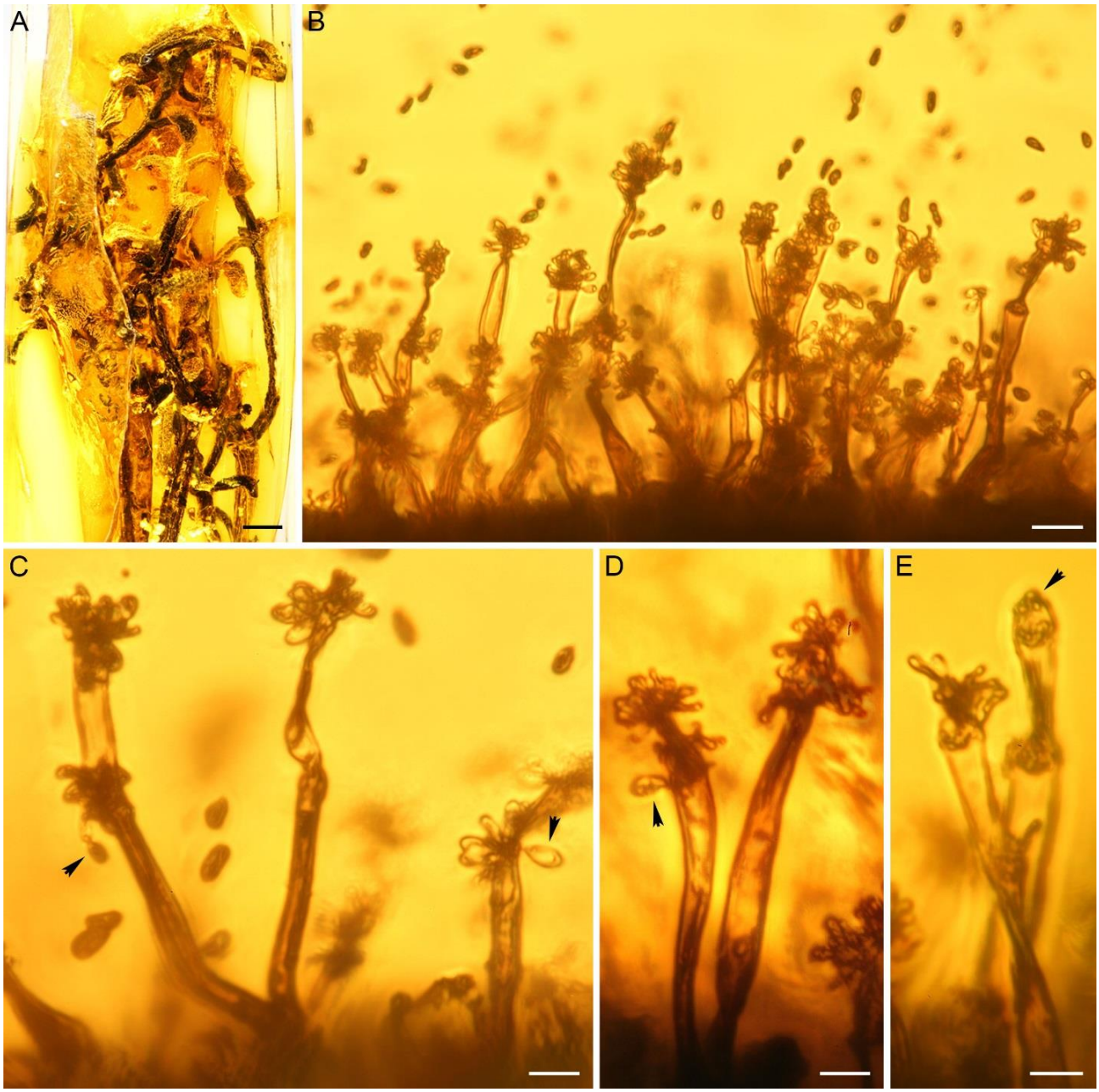

FIGURE 16. *Gonatobotryum*-like fungus growing on the dwarf mistletoe Arceuthobium viscoides (GZG.BST.21950). A, overview of the dwarf mistletoe branches. B, group of conidiophores and detached conidia. C, three conidiophores; the left arrowhead marks two conidia attached to each other and the right arrowhead points to a pale tear-drop-shaped conidium still attached to the conidiophore. D, two conidiophores with attached conidium (arrowhead). E, conidiophores with conidial scars (arrowhead). Scale bars represent: 1 mm (A); 20 µm (B); 10 µm (C–E).

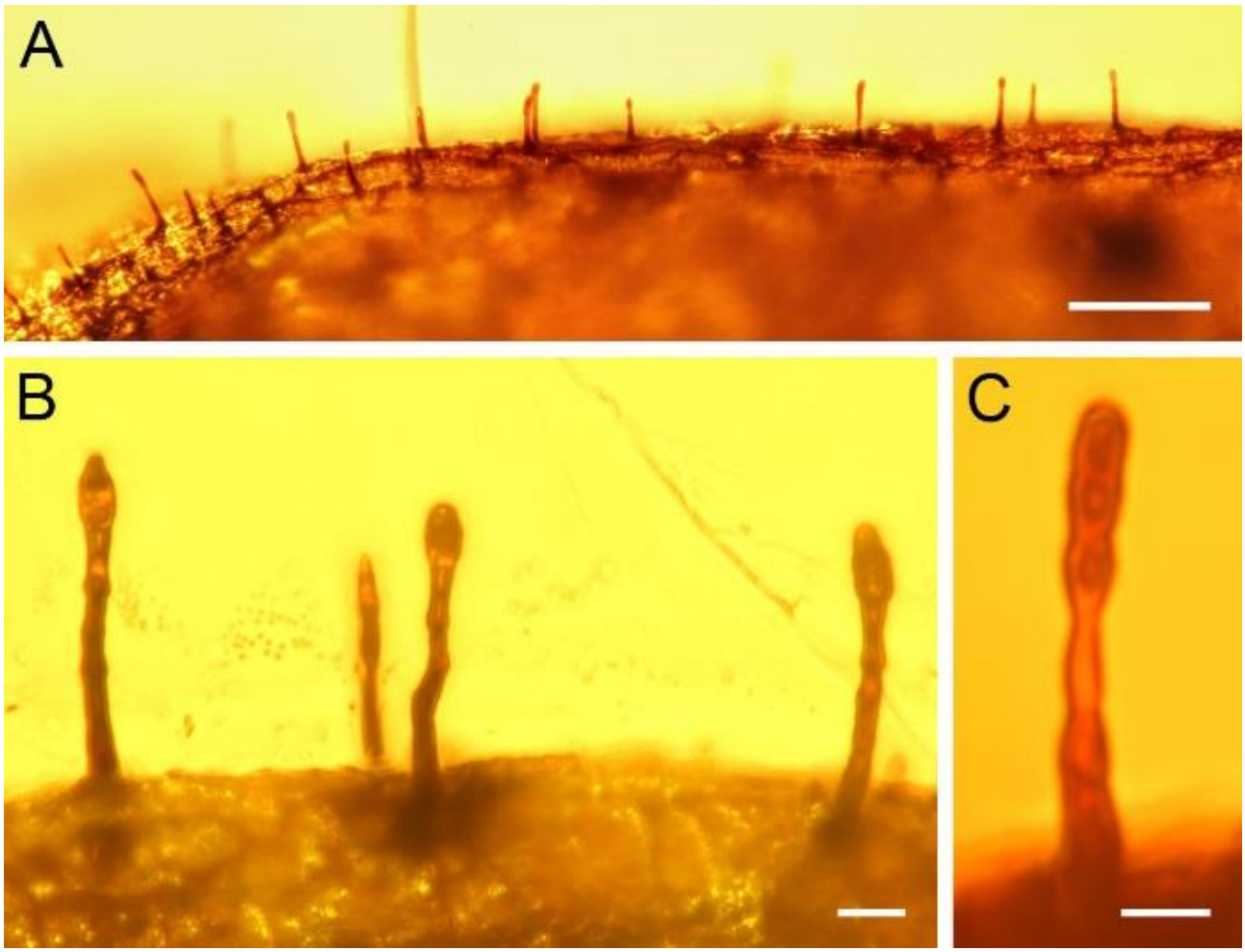

FIGURE 17. Hyphomycete with upright conidiophores (GZG.BST.24470). A, overview of conidiophores growing on a conifer leaf. B, conidiophores with conidia developing at the apices. C, conidiophore with a 2-septate conidium. Scale bars represent: 100 µm (A); 10 µm (B–C).

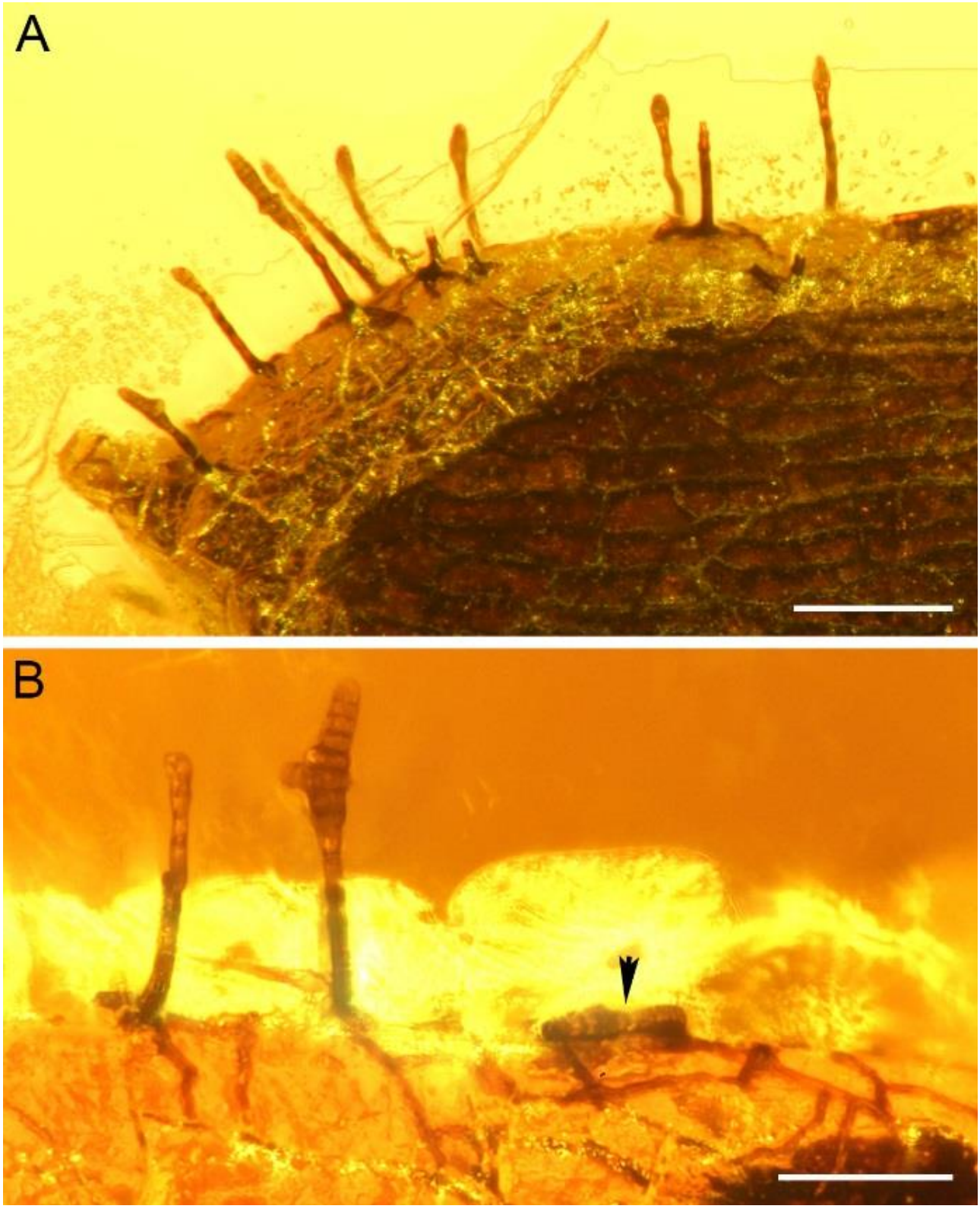

FIGURE 18. Hyphomycete with upright conidiophores (GZG.BST.24619). A, overview of conidiophores growing on a leaf. B, conidiophores with multiseptate conidia, the arrowhead marks a detached conidium. Both scale bars represent 100 µm.